THE
BIOLOGY OF CERTAIN FISHES
around the South West of England

A. **RAYS & SKATES** *(Raiidae)*

B. **MACKEREL** *(Scomber scombrus L)*

by

G. A. STEVEN

A.

RAYS & SKATES

(Raiidae)

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Rays and Skates of Devon and Cornwall. Methods of Rapid Identification on the Fishmarket.

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With 10 Figures in the Text.

In carrying out detailed investigations into the life-histories and distribution of the Rays and Skates around the extreme south-west of England, large numbers of commercial landings have had to be examined. On account of their size and cost, regular and adequate samples of Rays and Skates cannot be delivered at the laboratory, as is possible with such a small and inexpensive fish as the Herring, for example. It therefore has been essential to learn rapidly to distinguish the different species as they lie exposed for sale on the fishmarkets. This has been necessary not only to promote rapidity of work, but also to obviate all unnecessary handling of the fish, too much interference with which is apt greatly to annoy fishermen, salesmen, and buyers alike.

As Rays and Skates are laid out for sale in lots often of one hundred or more all with their lower surfaces upwards, the task of identifying the species without raising each fish to examine its upper side was found at first to be one of extreme difficulty, and accurate determinations were not possible. But gradually, as the result of concentration and much practice, it became possible to identify—simply from the characters discernible on their under surfaces—the eleven species of Raia landed at the various ports of Devon and Cornwall. Only when this facility has been acquired is it possible to make a general survey of the stocks present on the various fishing grounds by dealing rapidly, amidst the bustle and confusion of a busy market, with large numbers of fish in commercial catches.

In this paper, therefore, an attempt is made to enumerate and describe as clearly as possible the distinguishing features which have been found most useful for rapid identification of the species landed in this area. The descriptions are applicable to fishes of marketable size, and must not be expected to apply to stages less than about 30 cm. across the disc which do not ordinarily find a place in commercial landings. It will readily be understood, too, that minute details of obscure features, no matter how diagnostic they may be, will receive no mention.*

By careful observation of the characters here described any worker, even without previous experience of the family, should be able to distinguish with certainty and ease at least seven of the eleven species of Raia likely to be seen on the fishmarkets of Devon and Cornwall. The four others are less easily recognised, but a little patient practice should render possible the identification of them also from the characters normally visible on the under side. Nevertheless, even the experienced worker will encounter, from time to time, a fish which will require at least a glance at the upper surface to establish its identity. Occasionally, too, a specimen may occur which will be at once recognisable as either *Raia brachyura* or *R. montagui*—two short-nosed Rays often very similar in appearance—but cannot readily be assigned to its correct species even on careful examination of both sides. In such circumstances the easiest and most certain method of deciding the point, if several other undoubted examples of both species be available, is as follows :—

Lay out, back upwards, two separate lots of fish, one lot consisting of *R. brachyura* alone and the other of *R. montagui* alone. This done, place the doubtful specimen in the middle first of the one lot and then of the other ; it will then at once be obvious to which lot—and therefore to which species—it rightly belongs.

As indicated above, eleven species of Raia are landed more or less regularly at the various fishing ports of Devon and Cornwall. These are *R. montagui*, *R. brachyura*, *R. undulata*, *R. microcellata*, *R. clavata*, *R. naevus*, *R. circularis*, *R. fullonica*, *R. marginata*, *R. batis*, and *R. oxyrhynchus*.† These eleven species fall naturally into two main divisions :—

I. those whose under sides are of a decidedly dark ground-colour richly studded with black spots and which, for our present purpose, may be called " Black-bellied Species."

II. " White-bellied Species."

* For such detailed descriptions reference should be made to Clark's admirable monograph on the European species of Raia (**1**).

† Nomenclature according to Clark's monograph (**1**).

I. Black-bellied Species (Skates).

Only two species—*R. batis* Linn., and *R. oxyrhynchus* Linn.—are included in this division. They are separately distinguished as follows :—

RAIA OXYRHYNCHUS.	*RAIA BATIS.*
Long-nosed Skate. Bottle-nosed Skate.	Common Skate. Blue Skate.

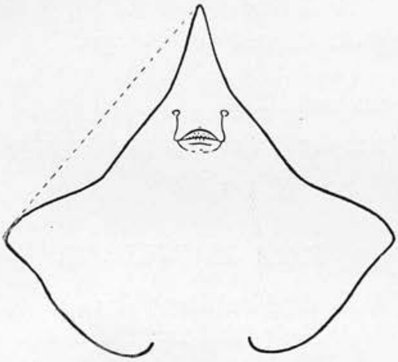

Fig. 1a.—*Raia oxyrhynchus*—outline of disc.

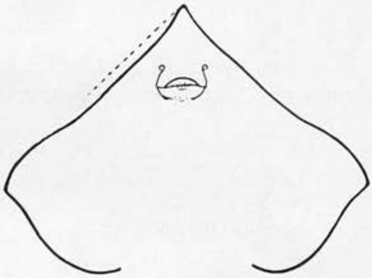

Fig. 1b.—*Raia batis*—outline of disc.

(Fig. 1a.)	(Fig. 1b.)
Snout very long, narrow, and pointed.	Snout relatively much shorter, broader, and less pointed than in *R. oxyrhynchus*.
Outline of anterior margin of disc strongly concave.	Outline of anterior margin of disc only slightly concave, often nearly straight.
Rarely reaches a width of 100 cm. across the disc.	Grows to a very large size, specimens of 150 cm. in width being not uncommon.

Large Skates are generally picked out by the fishermen and spread separately on the fishmarket. The smaller sizes, up to about 50 cm. across the disc, are laid out with the Rays interspersed indiscriminately among them.

II. White-bellied Species (Rays).

These fall into three distinct groups, according to the shape of the disc.

1. LONG-NOSED RAYS . .	*R. fullonica* Linnæus. *R. marginata* Lacépède.
2. CIRCULAR RAYS . .	*R. undulata* Lacépède. *R. naevus* Müller and Henle. *R. circularis* Couch.
3. SHORT-NOSED RAYS . .	*R. clavata* Linnæus. *R. brachyura* Lafont. *R. montagui* Fowler. *R. microcellata* Montagu.

1. LONG-NOSED RAYS.

The two species included in this group both have long and pointed snouts which mark them out at once from all the others.

RAIA FULLONICA.

Shagreen Ray.

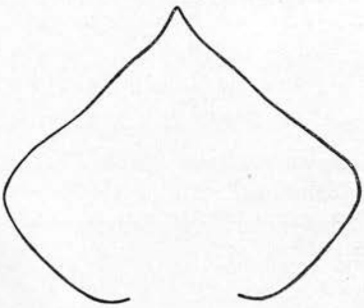

Fig. 2a.—*Raia fullonica*—outline of disc.

(Figs. 2a and 3.)

There is a well-marked groove (Fig. 3, G) in the middle of the upper jaw and a corresponding

RAIA MARGINATA.

Bordered Ray (Young).
White-bellied Skate* (Adult).

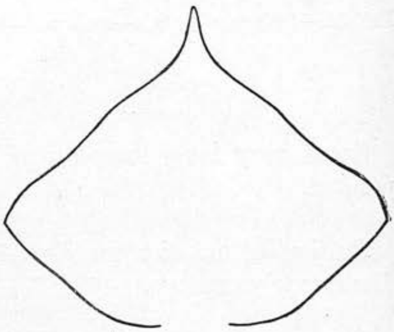

Fig. 2b.—*Raia marginata*—outline of disc.

(Figs. 2b and 4.)

Curve of mouth cleft quite regular.

* The large adults of this species are known to fishermen as "White-bellied Skates" and are laid out apart from the Rays, either by themselves or along with the large Blue and Bottle-nosed Skates. They are then very conspicuous because of the clear whiteness of their under sides, sharp snouts, and strongly undulated anterior disc margins.

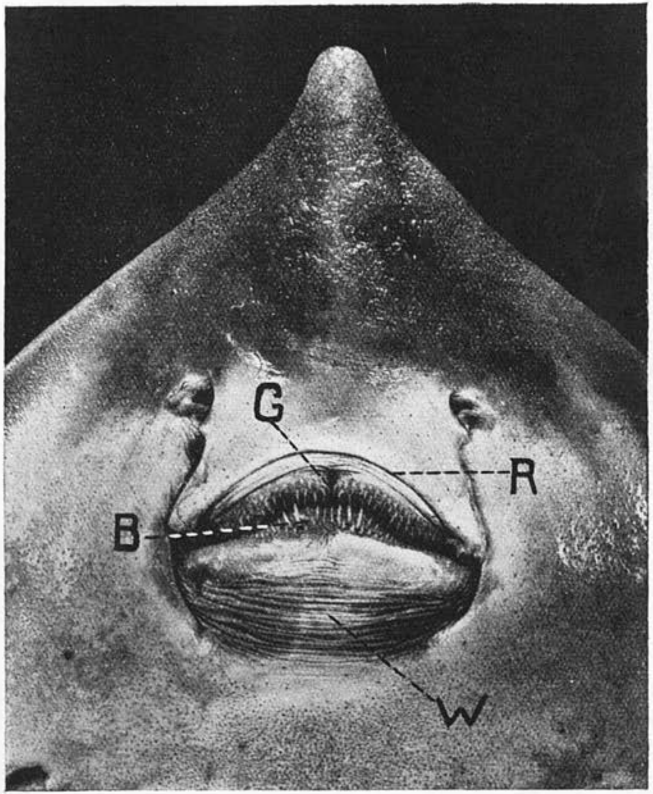

FIG. 3.—*Raia fullonica*—mouth and nasal regions.

R—pre-oral recess.
G—groove in middle of upper jaw.
B—" boss " in middle of lower jaw.
W—post-oral wrinkled region.

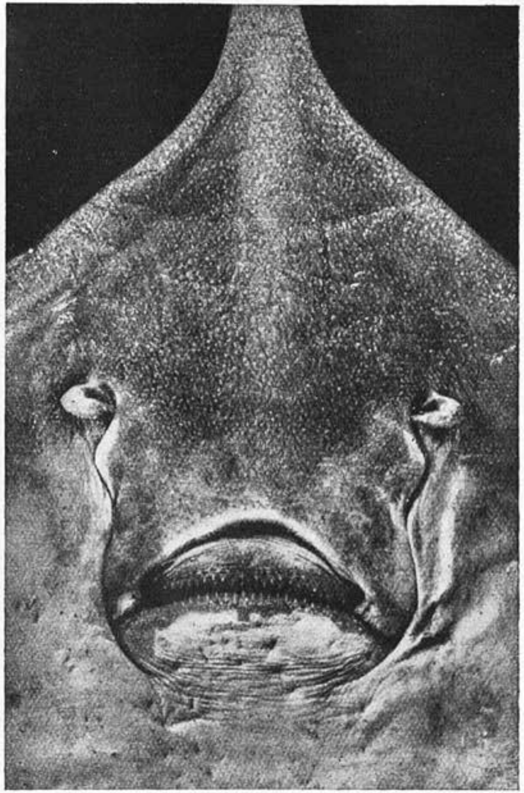

FIG. 4.—*Raia marginata*—mouth and nasal regions.

bastard skate. [illegible]

"boss" (Fig. 3, B) in the middle of the lower jaw which give the mouth cleft a very irregular outline.

Internasal distance appreciably less than width of mouth.

Anterior margin of disc not strongly undulated.

Ventral surface of tail white.

Seldom grows beyond 70 cm. in width of disc.

Internasal distance about equal to, or slightly greater than, width of mouth.

Anterior margin of disc strongly undulated.

Ventral surface of tail dark-coloured, sometimes nearly black.*

Adults very large, up to 150 cm. across the disc.

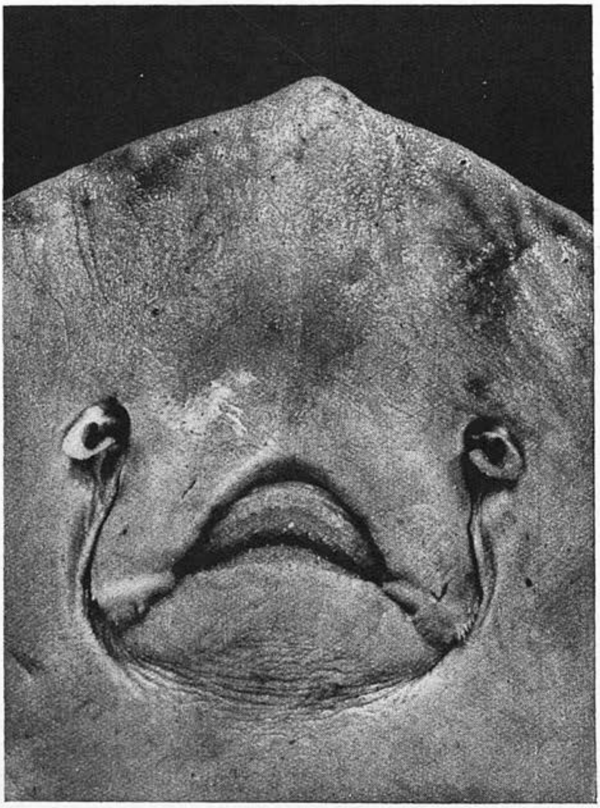

Fig. 5.—*Raia undulata*—mouth and nasal regions.

* In very young individuals there is a broad black band around the tips and along the posterior margins of the wings, but as this gradually disappears with age, it cannot be used with confidence for distinguishing the species.

2. CIRCULAR RAYS.

The three species which fall into this group all have the tips of their wings decidedly rounded and their snouts scarcely project in front of the main contour of the disc—characters which give them a typically "circular" appearance.

RAIA UNDULATA.

Marbled Ray.

(Fig. 5).

Arch of pre-oral recess high and acute.

Teeth flattened and close set, so that the separate rows are not discernible.

"Groove and boss" absent.

RAIA NAEVUS.

Cuckoo Ray.

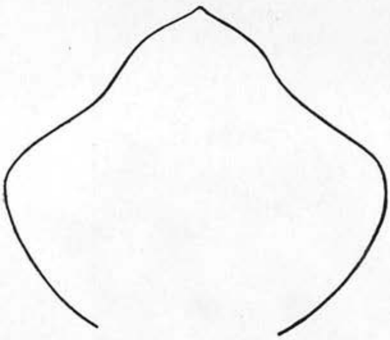

FIG. 6A.—*Raia naevus*—outline of disc.

(Fig. 6a.)

RAIA CIRCULARIS.

Sand Ray.

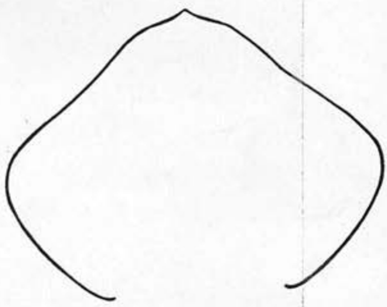

FIG. 6B.—*Raia circularis*—outline of disc.

(Fig. 6b.)

Arch of pre-oral recess low and obtuse.

Teeth long, pointed, and in widely separated rows which show up clearly.

"Groove and boss" generally discernible.

R. naevus	*R. circularis*
Anterior margin of disc strongly undulated.	Anterior margin of disc not strongly undulated.
Fish very thick and fleshy.	Fish always appreciably thinner than a specimen of *R. naevus* of the same width across the disc.
The smallest of the Devon and Cornwall Rays, seldom exceeding 40 cm. across the disc.	Adults commonly as much as 70–75 cm. across the disc.

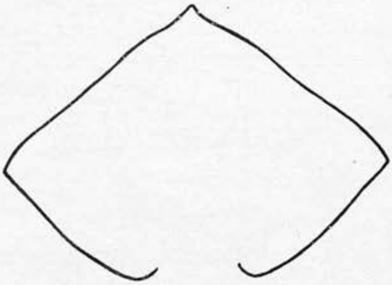

FIG. 7.—*Raia clavata*—outline of disc.

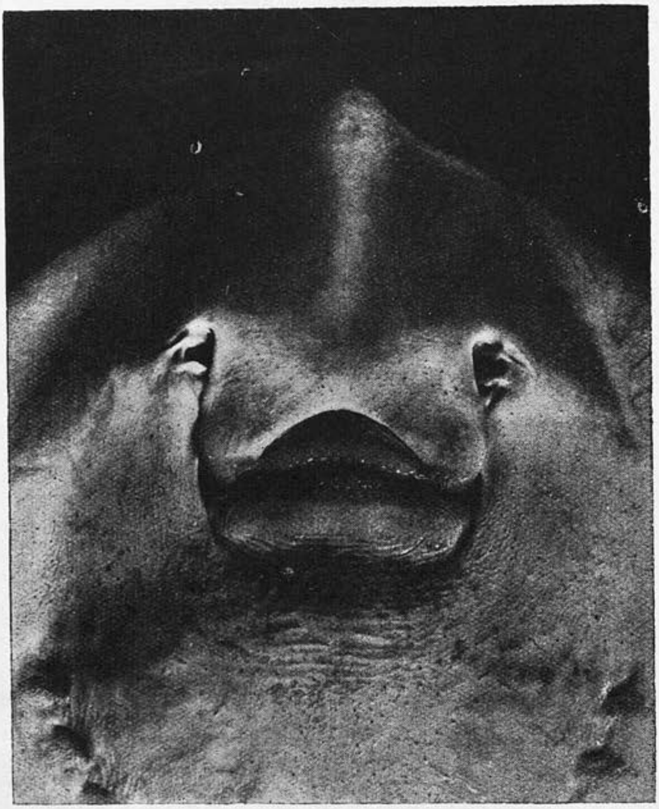

FIG. 8.—*Raia clavata*—mouth and nasal regions.

3. SHORT-NOSED RAYS.

In each of the four species included in this group, the general outline of the disc is typically diamond-shaped, due to the sharpness of the wing-tips and the presence of a short but well-defined snout (see Fig. 7).

RAIA CLAVATA.

Thornback Ray.

(Figs. 7 and 8.)

Arch of pre-oral recess high and acute.

Teeth large and distinct, markedly tessellated in adult females and in immature specimens of both sexes ; more pointed in adult males.

Internasal width about equal to width of mouth.

Lower surface with large spines and/or rough patches.

RAIA BRACHYURA.	*RAIA MONTAGUI.*
Blonde Ray.	Spotted Ray. Homelyn Ray.
(Fig. 9.)	(Fig. 10.)

Arch of pre-oral recess low and obtuse (except in adult males).

Internasal distance always less than width of mouth.

Large spines never present on lower surface.

Outline described by oro-nasal canals and hinder margin of post-oral wrinkled area (see Fig. 3, W) forming a wide with nearly straight or even concave base.	Outline described by oro-nasal canals and hinder margin of post-oral wrinkled area forming a more rounded with convex base.
Surface smooth all over except in large adults which may show some rough patches.	Surface smooth at all ages.
Often grows to 80 cm. in width of disc.	Seldom grows beyond 50 cm. across the disc.

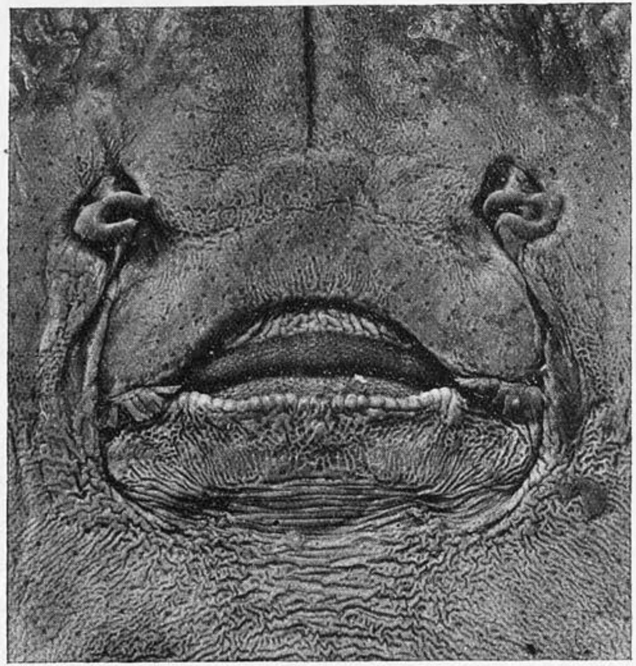

FIG. 9.—*Raia brachyura*—mouth and nasal regions.

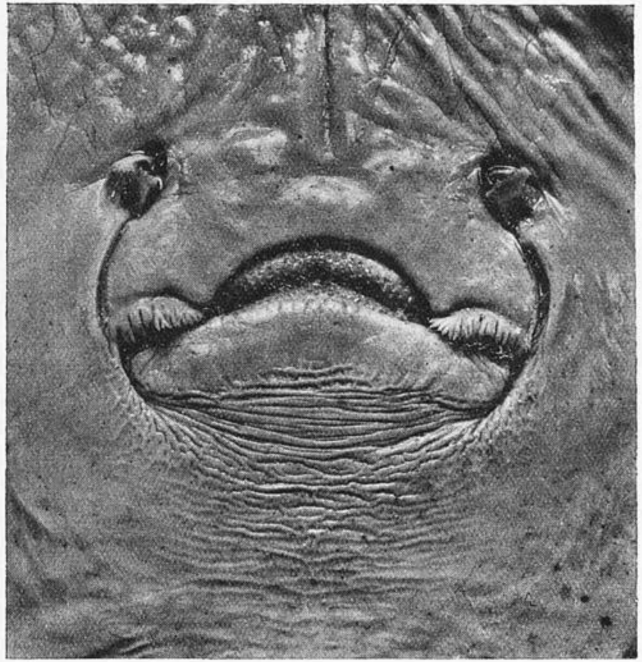

FIG. 10.—*Raia montagui*—mouth and nasal regions.

RAIA MICROCELLATA.

Painted Ray.

Resembles *R. montagui* in the characters of the mouth and nasal regions, but the pre-nasal area is covered with small spinulæ. In large specimens these are easily seen, but in smaller individuals it sometimes is necessary to touch the surface with the fingers in order definitely to establish their presence or absence.

Adults often grow to 70 cm. across the disc.

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Rays and Skates of Devon and Cornwall. II. A Study of the Fishery; with Notes on the Occurrence, Migrations and Habits of the Species.

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With 6 Figures in the Text.

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I. Growth of the Fishery.

There have been, in recent years, certain drastic changes in the sea fisheries of England and Wales. Not least among these has been the rapid rise in importance of Rays and Skates.

Prior to the beginning of the present century there was little or no demand for these Elasmobranchs in this country. Colonel Montague, writing in 1809, comments upon the immense quantities of Rays and Skates landed in Devonshire and states that they were then used chiefly for baiting crab-pots. In times of scarcity, however, some of the small ones were eaten by fishermen's families, *but were never exposed for sale.* Fifty years later this state of affairs had changed but little. Jonathan Couch, writing in 1862 (**3**, Vol. 1, p. 84), gives the following instructive account of fishing in the West of England at that time. " An adventure in the fisheries, at least in the West of England, is usually set on foot by some practical fisherman, who provides the boat and her outfit, and who himself acts as the principal fisherman ; and who seeks his profit as owner by what is called the boat share, which commonly amounts to a fifth part of the fish sold in the market : for the remainder he has a common share with his men. But other fishes will come to the hook besides those which find a place at fashionable tables, or the public are accustomed to buy, and which, indeed, are intrinsically as valuable as any which have a ready sale. The Grey Gurnard, Scad, Comber, Power, the Wrasses, Dogfish, Rays, and Skates, are in this class, and by the fishermen they are collectively known as rabble-fish, as being rejected from the market ; and they consequently fall to the lot of the fishermen themselves, who take them for the subsistence of their families, without deducting any portion for the boat share. The Skate is the largest, and, on the whole, the most important of these rejected fishes, and the Saxon word *Skitan*, to reject, is expressive of the fact of its being so. The same word is the parent of several expressions still in common use as significant of being thrown out, aside, or rejected." Again (*loc. cit.* p. 89), in writing specifically of the Blue Skate, *Raia batis*, he says, "The Skate is never the special object of the fisherman's search and when it chances to take the hook it may give him perhaps a greater amount of trouble than the prize can repay."

During the succeeding quarter of a century the fish-eating public in this country must gradually have grown aware of the value of Rays and Skates as food-fishes, for Day (**4**, Vol. II, p. 335), writing some time between 1880 and 1884, refers to Couch's account of Rabble-fish and adds the significant statement, "Things are altered now, much of this rabble-fish going to Billingsgate and other large inland markets."

Nevertheless, Rays and Skates even then were not considered to rank as food fishes. Cunningham, in his *Natural History of the Marketable Marine Fishes of the British Islands*, published in 1896, dismisses them with only a few words in the opening general section of the book. In the main part of the work dealing with the history of particular fishes they find no place. McIntosh and Masterman also, in their *Life Histories of the British Marine Food Fishes*, published in 1897, all but ignore the Raiidæ though they, too, discourse at length on such Teleosteans as the Gobies, Rocklings, Sticklebacks, and Blennies.

Towards the opening of the twentieth century, however, a definite fishery for Rays and Skates gradually arose and by 1906, the first year for which reasonably reliable statistical returns are available, no less than 384,953 cwt. of these fishes were landed at the various ports in England and Wales, to which total Devon and Cornwall contributed 44,618 cwt.

From that time onwards until the outbreak of the Great War in 1914, the annual landings remained fairly uniform, fluctuating only between 350,000 and 400,000 cwt. The prices, however, steadily rose—apart from two minor drops in 1909 and 1911—from an average value on landing of 11s. 2d. per cwt. in 1906 to 14s. 1d. per cwt. in 1913.

During the first five years of the post-war period (1919–1923) the landings of Rays and Skates in England and Wales steadily increased in total weight and total value. Since then, the quantity of fish landed has remained practically constant, averaging approximately 420,000 cwt. per annum (*vide* Fig. 1, p. 4).

Prices, however, gradually fell from the artificial peak produced by post-war conditions ; but the average value per cwt. over any full year has never fallen below 26s. 8d. (in 1927), a figure which is almost double that of 1913. At the present time prices are steadily rising (*vide* years 1927–30 in Table I, Column 4).

TABLE I.

England and Wales.

Total Weight of Skates and Rays landed (in cwts.) ; Total Value (in pounds) ; and Average Value per cwt—1906–30 inclusive.*

Year.	Weight (in cwt.).	Value (in £).	Average price per cwt.
1906	384,953	214,556	11/2
1907	378,773	216,170	11/5
1908	381,134	225,097	11/10
1909	415,704	230,591	11/1
1910	367,678	225,127	12/3
1911	351,729	200.972	11/5
1912	368,207	235,632	12/10
1913	359,446	253,729	14/1
—	—	—	—
1919	244,656	464,998	38/–
1920	356,869	625,534	35/1
1921	375,480	684,674	36/6
1922	438,505	608,048	27/9
1923	448,436	639,098	28/6
1924	422,161	599,761	28/5
1925	399,723	577,776	28/11
1926	364,523	539,905	29/7
1927	430,508	573,644	26/8
1928	424,724	573,238	27/–
1929	446,317	614,729	27/7
1930	435,818	638,896	29/4

Within the area under survey—Devon and Cornwall—the Ray and Skate fishery is of primary importance (*vide* Fig. 2, p. 5). The various species of the genus Raia collectively constitute the heaviest landings of demersal fish. In 1929 they formed no less than 35% of the total weight and 30% of the total value of all demersal landings for the year.†

* From the Ministry of Agriculture and Fisheries Statistical Tables of Sea Fisheries.

† It is of interest also to note that, with regard to quantity of fish landed in Devon and Cornwall in 1929, Dogfish come second to Skates and Rays, with 16% of the total by weight. That is to say that slightly over 50% by weight of all demersal fish landed in Devon and Cornwall in that year was Elasmobranch.

Actually, they are of still greater importance than even these figures indicate. Forming, as they do, the only large and staple fish supply within the area throughout the year, they play a large part in attracting buyers to the district and in keeping them there, thus helping to maintain a demand for other fish as well, with higher resultant prices.

II. Fishing Methods and Gear.

Rays and Skates are demersal fishes fitted by structure and habit for life on the sea floor. They may be fished by any of the usual methods

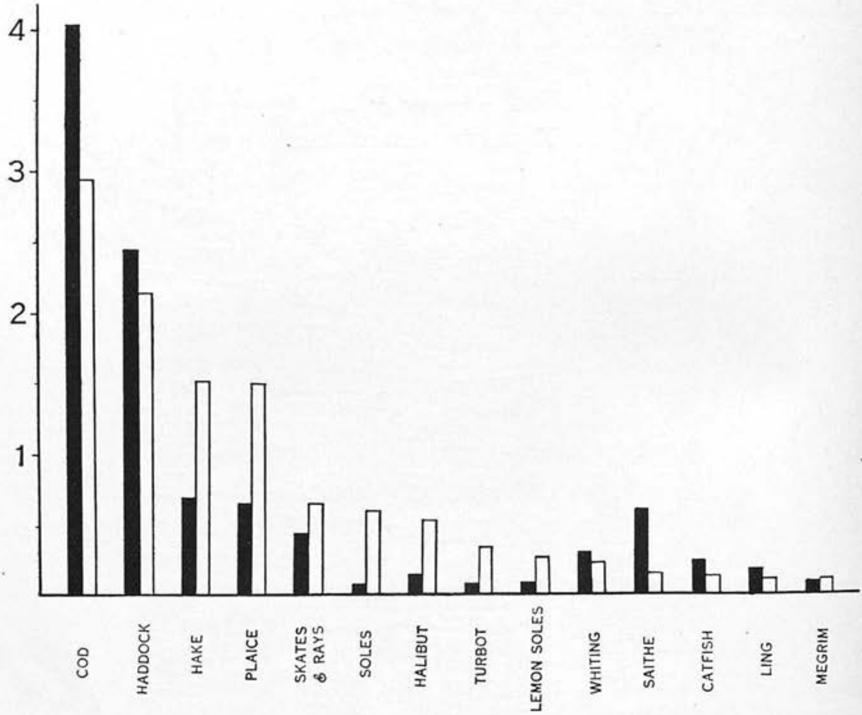

Fig. 1.—Graphical representation of the landings of the principal species of demersal fish of British taking landed in England and Wales in 1930, showing (*a*) total quantity (black columns) in millions of cwt., and (*b*) total value (white columns) in millions of pounds. *Note important position of Skates and Rays.*

employed in the capture of demersal species. In Devon and Cornwall they are caught in beam, V.D., and otter trawls, on long lines, and in set nets.

The main trawling ports are Brixham and Plymouth, from both of which fishing operations are carried out continuously over the whole year. From Brixham about 50 sailing smacks operate, all of which carry beam trawls. Nine small steam trawlers work from Plymouth and fourteen sailing smacks, the former equipped with V.D. and otter and the latter with beam trawls. At Padstow a fairly intensive trawl fishery is usually carried on during the first three or four months of the year by East-country steamers of the drifter-trawler type. There also work from each of these

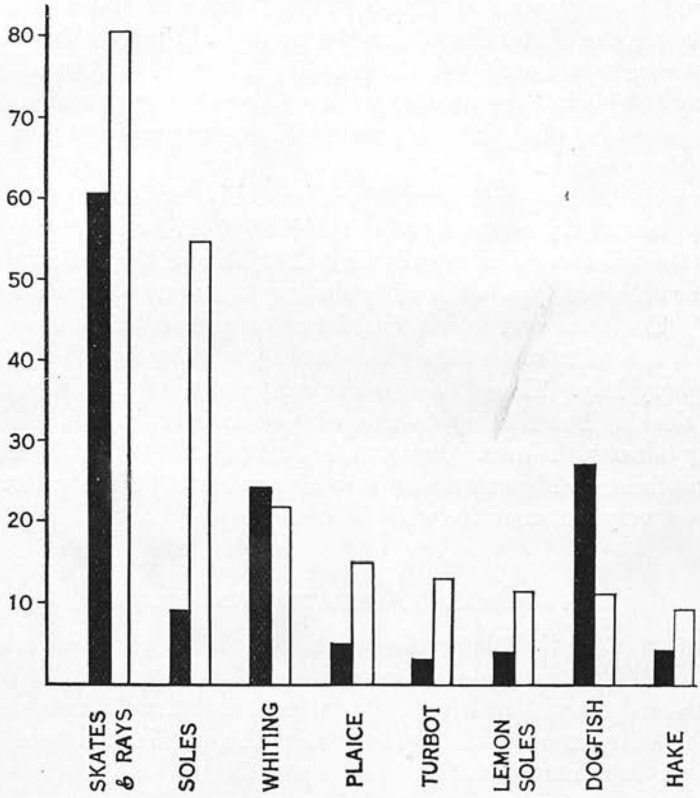

FIG. 2.—Graphical representation of the landings of the principal species of demersal fish of British taking landed in Devon and Cornwall in 1929, showing (*a*) total quantity (black columns) in thousands of cwt., and (*b*) total value (white columns) in thousands of pounds. *Note the leading position of Skates and Rays.*

ports and from the numerous other smaller harbours along the coast small motor trawlers which fish the inshore grounds.

At all seasons of the year Rays and Skates are caught on the usual trawling grounds with little variations in numbers except what can largely be attributed to weather conditions—a state of affairs which indicates a minimum of migratory movements, at any rate on a large scale. A certain amount of migration, however, does take place (*vide infra*, p. 18).

Long-lining is prosecuted mainly by Cornish fishermen with Newlyn as the main port. A certain amount of line fishing is also carried on from various other smaller ports on the Cornish coast, e.g. Looe, Mevagissey, and St. Ives. The line fishery continues for only part of the year, roughly from April till October. This is due not to any change or movement on the part of the stock of available fish, but to the movement of the fishing fleet which congregates at Plymouth from December till February to take part in the winter drift fishery for herrings. Even though no other fishery were to attract them, the long-line fishermen of Cornwall would scarcely be able to carry on successfully during the winter months owing to the small size of their vessels and the long distance from port of the line-fishing grounds.

The set-net fishery is at present peculiar to Plymouth and of particular interest in that it is seasonal and of short duration, lasting at most from about the middle of January till the end of March. The nets are of the fixed or anchored type set in fairly shallow water and acting as "tangle nets." The area over which this fishery is prosecuted is exceedingly limited, extending around the shore in shallow water from Yealm Point to Bigbury Bay. There is an inshore spring migration of large mature *Raia clavata* (Thornbacks) to this area (*vide infra*, p. 20), which are readily taken in the nets. Owing to the limited extent of the fishing area this net fishery will support only a small number of boats, but for these it proves very remunerative while it lasts.

III. Research Apparatus and Methods.

On account of their large size and heavy cost, regular and adequate samples of Rays and Skates cannot ordinarily be delivered at the Laboratory to be dealt with at leisure. In order to obtain sufficient data large numbers of commercial landings have had to be examined in considerable detail on the fish markets.

Rays and Skates, when exposed for sale, generally are spread out in lots on the fishmarket floor, all with their ventral surfaces uppermost. In order to avoid handling the fish—too much interference with which would not be tolerated by fishermen, salesmen, or buyers—it was necessary at the outset to learn rapidly and accurately to distinguish the various species landed in this area without raising each fish to view its dorsal side. After considerable practice this was found to be possible. The diagnostic characters which have proved most useful on the fishmarket have been described in a previous paper (Steven, **8**).

The problem of obtaining measurements of the fish also presented difficulties to be overcome. Amidst the bustling activity of a busy market it is quite impossible successfully to use an ordinary measuring board for several reasons. These are :

1. This method necessitates handling and moving every fish examined.

2. Amidst the conditions prevailing an adequate number of fish could not be dealt with in the limited time available while the fish are exposed for sale.

3. Any attempt to use such a board would prove a grave hindrance to the normal activities of the workers on the market.

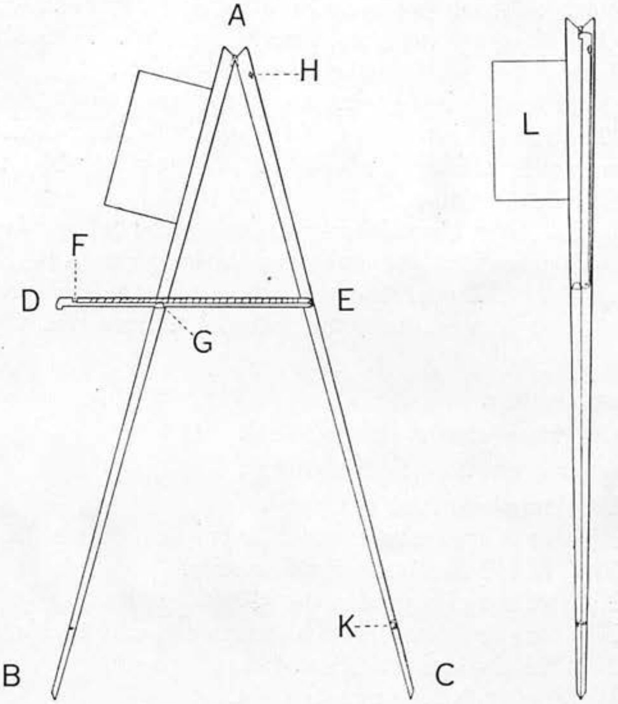

FIG. 3.—Measuring instrument used on the fishmarkets.
Left: open; Right: closed.

4. The use of an ordinary measuring board demands the services of two persons—one to carry out the measuring and another to record the data.

To overcome these difficulties an instrument was devised which renders possible rapid measurement of Rays and Skates spread out in lots, without handling or in any other way interfering with them, and at the same time enables a single unaided worker quickly and easily to record his data (Fig. 3).

The instrument is essentially a pair of large dividers 4′ 6″ in length. Twenty-two inches down from the hinge at the top an arm DE is fixed which can be moved around its point of attachment at E. When the instrument is in use the arm is dropped into a horizontal position and runs in a small slot G (on the leg AB) open at the top. The arm DE is bevelled along its upper edge and the sloping surface graduated to indicate in centimetres the distance between the points BC of the dividers.

Attached to the leg AB, in a convenient position near the top, is a small rectangular plate L measuring 12 inches by 6 inches. On this plate are carried numerous sheets of paper held in position by two rubber bands. All records are easily jotted down upon the uppermost sheet which is always at hand and firmly supported. Immediately it is filled it is removed and a clean sheet lies ready below.

When not in use the instrument is closed and the legs secured by the catch K. The arm DE is then swung upwards to lie along the leg AC and fixed in position by the small wing-nut H, the stem of which fits into a small recess F in the arm.

When possible, complete catches were dealt with; when this could not be done, as large random samples as could be overcome in the time available were examined. But whether the entire catch or only a representative part of it could be examined, the following information was always recorded.

1. Date of landing.
2. Locality where caught and gear used.
3. Total number of Rays in the landing.
4. (*a*) Total number of fish examined.
   (*b*) Number of species represented among fish examined.
   (*c*) Number of individuals of each species.
   (*d*) Number of males and females of each species.
   (*e*) Number of mature and immature males, as determined roughly from the size and condition of the claspers.*
   (*f*) Width of each fish across the disc.

In practice it was found necessary to use a more simplified system of notation than the usual male and female symbols (♂ and ♀) for denoting sex, and also to devise a method for recording mature and immature conditions in the males as indicated roughly by the size and condition of the claspers. The following scheme was adopted and proved highly successful. A measurement without any accompanying symbol denotes a female fish, a horizontal stroke above the figures denotes an immature male, while mature males were indicated by a ∧ over their measurements. Thus 49, $\overline{33}$, $\widehat{75}$, denote a female, an immature male, and a mature male of 49, 33, and 75 cm. respectively in width across the disc.

* The females could not be so divided as there is no external morphological difference between mature and immature individuals. Since this paper was written, however, a possible method of distinguishing between them without having to open the body-cavity for examination of the gonads, has been discovered. Further work is proceeding in order to test the accuracy of the method.

A typical fishmarket sheet is shown below :

5/3/30 S.T. . . . .
Fishing Mount's Bay (40–50 fm.)

Landed *ca.* 1200 small, 310 large } fish.

Sample of large fish.

R. brachyura ..	$\overline{58}$	69	59	$\overline{41}$	62	$\hat{69}$	55		
	71	79	49	$\overline{64}$	$\overline{55}$	54	53		
	62	$\overline{59}$	44	$\overline{59}$	65	77	75		
R. clavata	$\overline{49}$	49	44	55	$\overline{44}$	52			
	62	41	$\hat{59}$	51	63	61	55	59	
	59	57	$\overline{42}$	$\overline{55}$	59	49	$\overline{41}$		
	48	$\overline{47}$	47	$\overline{40}$					
R. fullonica	49	40	48	49	44	42	51		
R. montagui	41	$\overline{40}$	$\overline{39}$	44	47	$\overline{41}$	39	41	$\hat{42}$
	42	46	$\overline{40}$	$\overline{32}$	41	$\overline{39}$			
R. circularis	57	$\overline{59}$	$\overline{54}$	61	72	51	$\overline{52}$	48	46

From such a sheet the information set out under heads 1–4 *f.* above is then directly obtainable.

IV. Species Landed and the Numerical Contribution of each to the Fishery.

In the Ministry of Agriculture and Fisheries Statistical Tables of Sea Fisheries all the species of Raia are grouped together under the inclusive heading " Skates and Rays." From these returns, therefore, no information can be extracted concerning the separate contributions of the different species to the total " Skate and Ray " landings for either the country as a whole or for any statistical region within it. By the detailed examination of large numbers of fish in the manner described above, accurate information on this point so far as the markets of Devon and Cornwall are concerned has been sought.

It has previously been recorded by Clark (**1**, p. 581) that eleven species of Raia appear more or less regularly on the fishmarkets within this area. These are shown in Table II below.

TABLE II.

Species of Raia landed in Devon and Cornwall.

Scientific name.	Usual name in Devon and Cornwall.	More generally recognised common name.
1. *R. clavata* Linnæus.	Thornback Ray. Greeja (St. Ives). Roker (Commercial name).	Thornback Ray.
2. *R. montagui* Fowler.	Spotted Smoothback.	Spotted Ray. Homelyn Ray.
3. *R. brachyura* Lafont.	Blonde Ray. Smoothback Sand Ray. Calaber (St. Ives).	Blonde Ray.
4. *R. microcellata* Montagu.	(Painted Ray).	Small-eyed Ray.
5. *R. undulata* Lacépède.	(Marbled Ray).	Undulate Ray. Painted Ray.
6. *R. nævus* Müller and Henle.	Cuckoo Ray. Butterfly Ray.	Cuckoo Ray.
7. *R. circularis* Couch.	Sand Ray.	Sand Ray.
8. *R. fullonica* Linnæus.	Owl Ray (Newlyn).	Shagreen Ray.
9. *R. batis* Linnæus.	Common Skate. Blue Skate.	Blue Skate.
10. *R. marginata* Lacépède.	White-bellied Skate. Mule (St. Ives). *Owl (young).	Bordered Ray (young). White-bellied skate (adult).
11. *R. oxyrhynchus* Linnæus.	Long-nosed Skate (Bottled-nosed Skate).†	Long-nosed Skate.

The numerical compositions of the catches obtained by the two main methods of capture—long-lining and trawling—differ greatly from each

* When small, this Ray is not distinguished by the fishermen from *R. fullonica*.
† Should more correctly be applied to *R. marginata* (adult).

other, and from that of the total combined landings by all types of fishing vessels.

In long-line landings, the mean numerical composition by species is as follows (Table III) :—

TABLE III.

COMPOSITION OF LINERS' LANDINGS.

R. clavata	45%
R. fullonica	22%
R. nævus	15%
R. batis	10%
R. montagui	4%
R. circularis	3%
Total supplied by six species	99%

Three species, *R. marginata*, *R. brachyura*, and *R. oxyrhynchus*, each of which occurs in small numbers, supply the remaining 1%. *R. undulata* and *R. microcellata* seldom or never occur, even as single specimens, in line catches.

The landings by steam trawlers are made up as follows (Table IV) :

TABLE IV.

COMPOSITION OF LANDINGS BY STEAM TRAWLERS.

R. montagui	26%
R. brachyura	24%
R. nævus	24%
R. clavata	11%
R. fullonica	8%
R. batis	6%
Total supplied by six species	99%

The remaining 1% is made up by the five other species, all of which occur occasionally in the catches in small numbers.

Steam trawler Ray landings are generally separated for sale on the fishmarket into small and large fish, the " smalls " consisting of fish less than about 40 cm. (about 16 inches) across the disc. The compositions of the " small " and " large " fish differ fundamentally from each other. In the smalls the species occur as follows (Table V) :—

TABLE V.

Composition of Trawlers' "Smalls."

1.	R. nævus	30%
2.	R. montagui	29%
3.	R. brachyura	22%
4.	R. fullonica	8%
5.	R. batis	6%
6.	R. clavata	5%
	Total for six species	100%

Below is shown the totally different composition of the "large" fish (Table VI) :—

TABLE VI.

Composition of Steam Trawlers' "Large" Fish.

1.	R. clavata	33%
2.	R. brachyura	30%
3.	R. montagui	20%
4.	R. fullonica	7%
5.	R. circularis	4%
6.	R. batis	4%
	Total supplied by six species	98%

The remaining 2% is made up by five other species all of which occur in small numbers from time to time.

A third class of landings, from the point of view of numerical composition by species, is obtained by sailing smacks (beam trawls) and inshore motor trawlers (otter trawls). The catches by the last-named vessels are very similar to each other, both being drawn from shallower water than those of steam trawlers and liners, and are made up on an average as follows (Table VII) :—

TABLE VII.

Composition of Catches by Sailing Trawlers and Inshore Motor Trawlers.

1.	R. clavata	36%
2.	R. montagui	30%
3.	R. nævus	23%
4.	R. fullonica	8%
	Total supplied by four species	97%

Two species, *R. brachyura* and *R. microcellata*, supply between them most of the remaining 3%, but all the other species present in the area occur in small numbers from time to time.

To obtain the numerical composition by species of the total landings within the area is not possible by direct methods as records of the total number of fish landed by the different types of vessel are not available. The weight of fish landed, according to the different methods of capture, is, however, obtainable from the Ministry of Fisheries official records of landings at major ports.

These reveal that approximately 37% by weight of the total trawled fish landed at the major ports in Devon and Cornwall is caught by steam trawlers and 63% by weight by wind and motor trawlers. Again, it has not been possible to obtain any accurate determination of the relation between the number of fish landed by the various methods of capture and their total weight. But from general observation of the landings it would appear that for the two classes of landings by trawlers the number/weight relations are not widely different. Calculating on this assumption, the numerical composition by species of the total *trawl* landings at the major ports of Devon and Cornwall is as follows (Table VIII) :

TABLE VIII.

COMPOSITION OF TOTAL TRAWL LANDINGS.

R. montagui	29%
R. clavata	27%
R. nævus	24%
R. brachyura	10%
R. fullonica	8%
Total produced by five species	98%

The six other species in small numbers make up the remaining 2%.

The total trawled fish forms 42% by weight of the complete total of Rays and Skates landed—by all methods of capture—and liners produce 58% of that total. Here, however, it is certain that trawled landings contain a greater mean number of fish per cwt. than do liners' landings.

To calculate the percentage numerical composition of the total landings for the area, therefore, on a basis of 42% trawl and 58% line fish will give a slightly higher value than the true one to those species which bulk largely in liners' landings. Bearing this source of error in mind, the figures obtained by calculating on this basis are nevertheless instructive. These are as shown below (Table IX) :

TABLE IX.

COMPOSITION OF TOTAL LANDINGS AT MAJOR PORTS OF DEVON AND CORNWALL.

R. clavata	37%
R. nævus	19%
R. fullonica	16%
R. montagui	15%
R. batis	7%
R. brachyura	4%
Total supplied by six species	98%

The remaining five species collectively make up the remaining 2% of the total.

The combined results for the most important species are summarised in Table X.

TABLE X.

PERCENTAGE NUMERICAL COMPOSITION OF LANDINGS (SUMMARY).

		Steam Trawlers.			Wind and inshore	Total	Total Land-
	Liners.	Large.	Small.	Total.	motor.	Trawled.	ings.
R. clavata	**45**	**33**	5	*11*	**36**	**27**	**37**
R. nævus	*15*	—	**30**	**24**	**23**	**24**	*19*
R. fullonica	**22**	7	8	8	8	8	*16*
R. montagui	4	**20**	**29**	**26**	**30**	**29**	*15*
R. batis	*10*	4	6	6	—	—	7
R. brachyura	—	**30**	**22**	**24**	—	*10*	4
R. circularis	3	4	—	—	—	—	—

V. OCCURRENCE AND DISTRIBUTION.

Within the area under survey Clark (**1**, p. 581) gives the following general information regarding the distribution of the species.

"Numbers 1, 2, 3, 4, 6, 8, 9 (*vide* p. 10 *supra*) are of frequent occurrence in the neighbourhood, and are taken at all stages. Numbers 5, 7, 10, 11 are periodic in their appearance, but the young of 5 and 10 occur commonly on the outer grounds.

Numbers 7, 10, 11 increase in frequency with deeper water towards the western end of the Channel."

From the data set down in section IV it will be seen that *R. clavata* is the most abundant species among the total landings. It is, in fact, the most generally distributed species at all depths, and on all kinds of bottom, but generally showing a decided preference for rough ground. Clark (**2**, p. 25) states its bathymetric distribution to be "shallow water to moderate depths," but gives no actual figures. At the western entrance to the English Channel it is abundant down to 80 fathoms, and appears not to diminish in still deeper waters, although definite data from greater depths in this particular region are not at present available. But that it is common down to over 100 fm. is shown by the results obtained during a trawling cruise in the *George Bligh* in August of last year. A series of nine trawl-hauls, each of four hours' duration, was taken roughly 80 miles N.N.W. of the "Bull" in various depths from 89 fm. down to 180 fm. As the ship was trawling specially for Hake, Rays did not figure largely in the catches, but some were present in every haul except one. Of the species taken, *R. clavata* was always most abundant down to roughly 100 fm. and was not absent in depths of from 160–180 fm. Beyond about 100 fm., however, *R. fullonica* became definitely more numerous and *R. clavata* less numerous in the catches (Table XI, p. 16).

R. brachyura is also fairly abundant in the Channel area but is practically absent from liners' catches, although numerous in trawl landings—especially those of steam trawlers. The reason for this is twofold.

(1) The main long-line fishing fleet which operates from Newlyn, fishes generally in from 60–80 fm. of water or even more. *R. brachyura*, however, according to Clark (**2**, p. 16) is confined to depths less than about 60 fm. This species has a decided preference also for sandy ground, such as is suitable for trawling, and therefore is taken by trawlers whose main fishing grounds lie in depths of under 60 fm.

(2) Liners can and do work on rough ground such as is favoured by *R. clavata* but not by *R. brachyura*, and avoid the softer trawling grounds on account of the danger to their lines. This also tends to prevent their taking *R. brachyura* in any numbers.

The periodic appearance of *R. undulata* and *R. microcellata* on the fish-market (Clark, **1**, p. 581) does not appear to be due to any periodicity in the movements or occurrence of the fish themselves. These two species are very restricted in their distribution, *R. undulata* being confined to a trawling ground 18–20 miles outside the Eddystone* and *R. microcellata* to a few sandy bays and estuaries. It is because of their very restricted distribution that those two species do not appear regularly in the landings. When the grounds on which they do occur are visited they seldom fail to appear in the catches.

R. nævus is most abundant in this area between 35–60 fm. No useful information can so far be added regarding the general distribution of the other species.

It has been found that unispecific shoals and unisexual shoals of one

* An occasional specimen may sometimes be taken off Start Point.

TABLE XI.

Serial number of haul.	Depth in Fathoms. (a) on shooting.	(b) on hauling.	(c) mean of a and b.	Rays present in Trawl. R. clavata.	R. fullonica.	R. nævus.	R. batis.	R. oxyrhynchus.
2	89	102	95½	5	—	—	—	—
1	120	89	104½	15	5	2	2	2
4	115	96	105½	45	15	3	2	1
3	102	115	108½	5	9	2	10	2
9	110	120	115	—	—	—	—	—
5	96	158	127	43	12	—	4	—
8	162	110	136	9	11	—	3	—
6	145	145	145	2	20	—	3	—
7	180	162	171	12	57	—	1	—

Extra haul off Black Rock—53° 40′ N. : 11° 20′ W.

						R. circularis.
17	137	124	130½*	7	26	4

* Trawl was fishing for part of the time in at least 150 fm.

species occur—as for instance is shown for *R. clavata* landed from the Ray net fishery at Plymouth (*vide* p. 22 *infra*). Liners' catches, too, occasionally furnish evidence of this segregation. On 23rd August, 1930, a liner which had been fishing 45 miles S.W.$\times$W. of Carn Du Point near Mousehole, had an almost blank haul, catching only nine fish. All these nine were *R. fullonica* and *all females*.

On 3rd June, 1930, a small inshore trawler fishing near Newlyn brought in 205 Rays, 183 of which were *R. brachyura*. Of these 152 were male and 31 female.

There can be little doubt, therefore, that there do occur unispecific shoals which at times may be almost if not entirely unisexual.

Such separation of species, however, unless the shoal be very large and cover an extensive area, or if small, be alone in a fairly large area, is not noticeable as a general rule in trawl landings as there is no indication in the catch of the order in space and time in which the captured fish were taken. When emptied on deck the contents of the "cod end" are all thoroughly mixed up. Nevertheless, an almost completely unspecific and unisexual haul was made by a steam trawler in Mount's Bay in March, 1930 (*vide* p. 23 *infra*).

As a general rule, on most of the larger fishing grounds, although one species may predominate, several species are present. In those circumstances do the various species mix indiscriminately or do the members of each species tend to keep together? An attempt to answer this question was made by taking an accurate census of every fish which came up in three hauls of a full fleet of long-lines ordinarily used by a Cornish long-liner. On the vessel in question the fleet consists of 24 baskets of line, each basket carrying roughly from 110–120 hooks about 11 feet apart.

If the various species are in separate shoals or groups there should be a tendency for the same species to appear more or less together on the same part of the line. Any such grouping will always tend to be obscured, of course, by the fact that the lines remain on the sea floor for anything up to six hours at a stretch. Therefore, even though at the outset there may be a definite distribution of the species along the line, other fish, or shoals of fish, will come along and take the hooks which have not previously been occupied. Thus the distribution of fish caught on the lines at any particular point of time unless they occupy adjacent hooks—which is unlikely—will be obscured by those which were hooked previously and by those which subsequently come along and are caught.

The possibility must also be recognised that purely as the result of chance, two or more fish of the same species may occur together here and there on the line though the population be entirely and indiscriminately mixed.

An examination of the distribution of fish along the above-mentioned lines reveals a definite tendency for the same species to appear more or less together on the line. This grouping is too pronounced to be explained purely as the result of the laws of chance.

In Figure 4A is shown diagrammatically the catch of fish on a continuous section of line 1½ miles in length, hauled during the forenoon of 22nd July, 1931, from a fishing ground roughly 80 miles S.S.W. of Mousehole, near Newlyn, Cornwall. Each short vertical stroke denotes a hook which came up empty. A stroke produced downwards indicates a hook on which a fish of some kind was taken, while a stroke produced both downwards and upwards and ending above in a large dot denotes one on which *R. montagui* was taken. It will at once be seen that this fish shows a very definite grouping on this part of line. A similar grouping of *R. montagui* is shown in Figure 4B on a half-mile stretch of line hauled during the afternoon of 23rd July, 1931, on slightly different ground.

In Figure 5 is shown a continuous stretch of line 2½ miles long with the upwardly extended strokes denoting *R. nævus*, this being part of the same haul as the second one mentioned above. Here again a very definite grouping of the fish is seen. These results agree with other more general observations made at sea by the author when, however, a definite record of each hook and fish could not be made.

It appears, therefore, that, on the sea floor, where various species of Raia are present within a limited area at the same time, the species do not mix indiscriminately but segregate into unispecific groups or shoals.

VI. Migrations.

As yet little is known regarding the migrations and shoaling habits of the Raiidæ. What little information there is on record applies mainly to *Raia clavata*, perhaps because its movements are more marked than those of the other species or perhaps because it is the most generally distributed and most abundant Ray in inshore shallow waters and at moderate depths down to at least 80 fm. Meek (**5**, p. 41) states definitely that there is, in this species, a periodical migration inshore in summer and into deeper water for the winter. Unfortunately he gives no actual data as to depths. At the western entrance to the Channel, there is little evidence of such a wholesale inshore migration in summer at any rate within the area inside the 80 fm. line. The long-liners, which are responsible for over 50% of the total Ray landings in Devon and Cornwall, fish throughout the summer months only, mainly in depths of from 60–80 fm., and the present tendency is for the boats to go still farther offshore into ever deeper water in order to maintain the level of their catches.

Certain conditions described by Murie (**6**, p. 166), however, for the Thames Estuary are borne out by observation in this area. According to

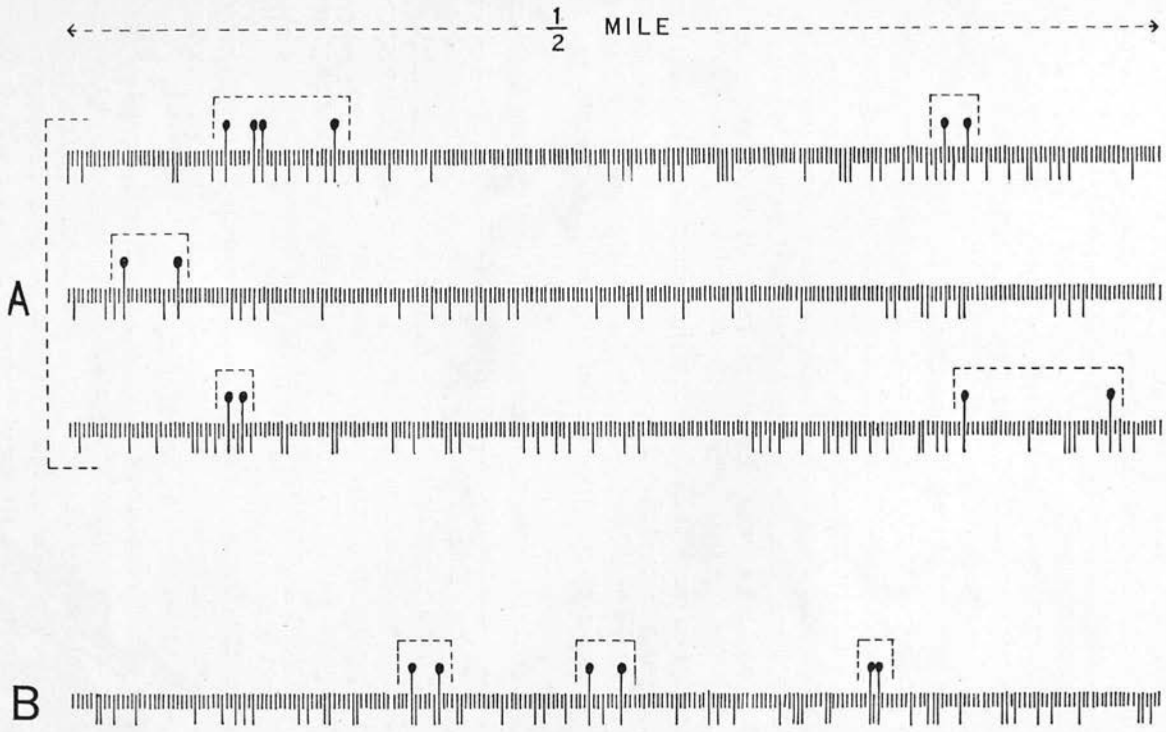

FIG. 4.—A. Diagrammatic representation of the distribution of *R. montagui* and other fish on a continuous stretch of $1\frac{1}{2}$ miles of long-line—22nd July, 1931. For explanation see text, p. 18.

B. Distribution of *R. montagui* on $\frac{1}{2}$ mile of long-line, 23rd July, 1931.

this author the Thornback is captured in shallow water almost at all seasons, especially during its early stages.

Examination of steam trawlers' fish landed on Plymouth market indicates clearly that this statement holds good for this area also. It is the usual custom among steam trawlers on landing Rays to separate them into " small " and " large " fish—the former consisting of fish under about 40 cm. across the disc and the latter of the larger ones. Among their small fish very few *R. clavata* are to be found at any season, giving an average of not more than 5% over the year. Among their larger fish, however, *R. clavata* forms about 33% of the total (*vide* Table X, p. 14).

The steam trawlers fish mainly in water of from 40 to 60 fm. in depth. The Ray landings of vessels fishing inside the 30-fathom line, however, consist mainly of *R. clavata*, the majority of which are of small and medium size, such as would be included in the " smalls " of steam trawlers.

Of 943 fish landed from shallow water by the research vessel *Salpa* during 1930–31 and identified and measured, 83% were *R. clavata*. Of these, 82% consisted of young individuals under 40 cm. in width across the disc.

The explanation seems to be that the young fish are hatched in shallow water and remain there during their early stages of growth, moving out into deeper water when they have reached a size of 40 cm. or over across the disc. Corroborative evidence on this point is being sought by means of marking experiments.

Migrations, either feeding or spawning, or both, do also occur, however, among the adult Thornbacks. Murie (**6**, p. 167) states that, " when long-lining in the Wallet (Thames Estuary), Rokers were few at the beginning of the fishing season, but as the sprats came about so did the Rokers multiply. They would be from 18 inches to 2 feet wide, length in proportion, and more big than small ones. As an instance of a good catch, some thirty years back (1870?) in the Barrow Deep one morning, on 28 lines, 190 great Rokers were hooked, besides several lines being lost through weight of fish on them."

It is evident that, in the above-mentioned areas of the Thames Estuary, the adult Thornbacks appear for a time in large numbers probably feeding on sprats—i.e. they show a feeding migration.

A strikingly similar inshore migration of adult Thornbacks takes place every spring in the vicinity of Plymouth. Each year, usually about the middle or end of January, while herrings are still abundant, large numbers of *R. clavata* congregate in fairly shallow water—inside the 22-fm. line—around the shore to the eastward of Plymouth Sound from Yealm Point to Bigbury Bay, and give rise to the set-net fishery already mentioned.

The landings from this net fishery present certain features of great interest. The first fish to arrive (as shown by the landings—Table XII)

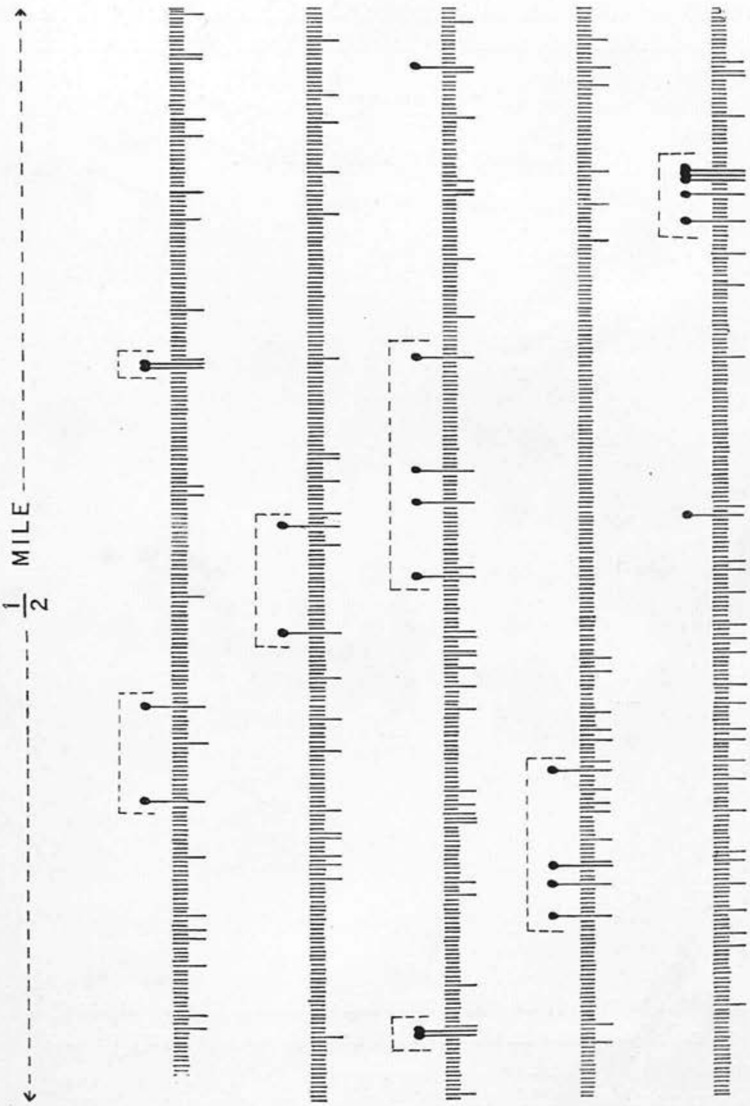

FIG. 5.—Distribution of *R. nævus* on a continuous stretch of $2\frac{1}{2}$ miles of long-line—23rd July, 1931.

are almost entirely females—all fully grown gravid fish nearly, but not quite, ready to deposit their eggs. In a few weeks, adult male fish begin to appear in increasing numbers and finally landings may consist almost entirely of adult males, the females having departed and the males having taken their place. When this happens, the fishery is nearly at an end. These male fish do not remain long behind the females which have already left the area.

TABLE XII.

LANDINGS FROM RAY NETS.

	R. clavata.		*R. brachyura.*		*R. batis.*	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
			1930.			
February						
20	10	192	—	—	—	—
21	10	198	—	—	2	—
24	34	199	—	—	3	3
March						
4	1	33	2	—	2	4
8	20	44				
10	2	47	6	—	—	—
11	67	37	—	—	—	—
12	28	41	—	—	—	—
15	38	—	1	—	—	—
January			1931.*			
12	2	159	1	—	—	—
13	—	121	1	1	—	—
16	2	49	—	—	—	—
19	2	198	3	—	—	—
20	5	156	1	—	—	—
22	1	75	2	—	—	—
23	17	123	2	—	—	—
February						
3	2	77	12	3		
4	—	121	2	2		

All the fish move off before "spawning" takes place. Although the females landed all contain almost ripe ova, in scarcely any of them are egg capsules to be found.

This congregation of Thornback Rays around the shore from Yealm Point to Bigbury Bay, upon which the Plymouth Ray net fishery depends, is therefore an inshore feeding migration of mature adult fish (*Vide* pp. 23 and 24).

* Owing to stormy weather the fishery this year came to a premature close.

There is evidence of similar brief inshore migrations in early spring at other points along the south Cornwall coast. In March, 1930, a steam trawler after fishing with little success for a week "off the Wolf" moved into Mount's Bay. There, in 25–30 fm. of water, on the night of Saturday–Sunday, 15th–16th March, between the hours of 7 p.m. and 2 a.m. she caught 210 large Rays, 207 of them being *R. clavata*,* of which every one, without exception, was a large female. Another trawler, fishing at the same time just outside in 45–50 fm., had the usual mixed trawl catch.

Certain fishermen say that these large Rays appear every year off Falmouth, but the trawlers cannot always get at them because they go too far in. Unfortunately, there is no inshore Ray net fishery there from which to obtain corroborative evidence. Nor is there such a fishery at any point around the coasts of Devon and Cornwall, except at Plymouth.

Evidence of a somewhat similar migratory movement on the part of *R. brachyura* is furnished by the catches of a small motor liner fishing from Newlyn. This vessel, being unable to go as far to sea as the regular fleet of larger liners working from the port, normally fishes on a small sandbank close inshore.

On 4th June, 1930, this small liner landed 853 Rays, consisting of 824 *R. brachyura* (and 29 *R. montagui*), not a single fish being more than 50 cm. across the disc. In August of the same year, this vessel, fishing on the same bank with the same gear, was bringing in catches consisting again almost entirely of *R. brachyura*, and all 65–75 cm. in width across the disc.

As it does not seem possible for a growth of 15–25 cm. to have taken place in two months, it must be assumed that the large fish had migrated to the bank from elsewhere and that the smaller fish had moved away. Unfortunately, no observations on the landings at Newlyn were possible in the period between June, when the immature fish were being landed, and August, when the large mature fish had taken their place.

VII. Food and Feeding.

As is already well known, young Rays feed very largely upon small crustaceans, especially Amphipods and Crangonids (Clark, **1**, p. 635). In the vicinity of Plymouth the Amphipod *Ampelisca spinipes* is of primary importance, being present in large numbers on certain grounds (Steven, **6**, p. 681). As the fish increase in size they turn their attention to larger crustacea such as Upogebia, Portunus, and Corystes, and—in certain species at least—to fish.

Adult Thornbacks, however, sometimes feed entirely on fish. The

* The three others were large male *R. brachyura*. It is interesting to note that, in nearly every catch of *female R. clavata* from the Ray nets there is also nearly always present one or two *male R. brachyura*.

large Rays of this species taken by the nets already mentioned (p. 20) were in both 1930 and 1931 found to be feeding exclusively on herrings and sprats. Of several hundreds of stomachs examined, not one was found to contain anything but fish, mainly herring (sometimes as many as six in one stomach), and not more than half a dozen empty stomachs were encountered. Several large *R. brachyura* and a few large *R. batis* taken in the same locality also had their stomachs full of herrings. One of the latter, a female measuring 143 cm. across the disc, contained no less than nine large fish.

Other fish, commonly including Rays, also enter largely into the diet of adult *Raia batis*.* Of 41 stomachs of these fishes ranging from 89 cm. upwards in width of disc, examined on and between 25th and 30th July last year, 13 contained one or more Raia sp. Those specimens of which the species could be determined consisted of *R. nævus* and *R. montagui*, with one doubtful *R. clavata* among them. The full results of the examination of the stomachs are tabulated below.

FOOD OF SKATES (*R. batis*).

25th July, 1930.

Serial No. of Fish.	Width across disc (in cm.).	Food in Stomach.
1	101	*Raia nævus*
2	94	*Scyllium canicula* *Homarus vulgaris*
3	124	Empty
4	145	*Lophius piscatorius*
5	100	Raia sp.
6	108	*Acanthias vulgaris*
7	129	Empty
8	125	*Eledone cirrosa*
9	93	*Raia nævus*†
10	90	*Eledone cirrosa*
11	105	*Pleuronectes limanda*
12	98	*Lophius piscatorius.*
13	110	Empty
14	99	*Raia nævus*
15	91	Raia sp. (? clavata)
16	97	Empty
17	102	*Caranx trachurus*
18	100	Raia sp. remains

* See also Murie, **6**, p. 165.

† This fish had been caught on one of the hooks of a long-line. It was then swallowed by a Skate which was itself also caught on the same hook.

Serial No. of Fish.	Width across disc (in cm.).	Food in Stomach.
19	104	Empty
20	98	Empty
21	96	*Acanthias vulgaris*
22	95	Empty
23	109	*Cancer pagurus* *Eledone cirrosa*
7th July, 1931.		
24	116	*Acanthias vulgaris*
25	104	*R. nævus*
26	123	*R. montagui*
27	119	Empty
30th July, 1931.		
28	121	*Cancer pagurus*
29	104	*R. montagui*
30	98	*Cancer pagurus*
31	89	*Eledone cirrosa*
32	96	*Acanthias vulgaris*
33	125	Empty
34	139	Empty
35	146	Empty
36	144	*Raia nævus* *Trigla cuculus*
37	142	*Clupea pilchardus* *Cancer pagurus* *Pleuronectes microcephalus*
38	119	Empty
39	126	*R. nævus*
40	98	*R. montagui*
41	94	*Cancer pagurus* Raia sp. remains

Nine large *Raia marginata*, 90–135 cm. in width across the disc, examined at the same time, were all found to have empty stomachs. The food of six *R. oxyrhynchus*, 83–114 cm. across the disc, included *Cancer pagurus*, *Atelecyclus septemdentatus*, *Corystes cassivelaunus*, other crustacean remains, Trigla sp. and *Callionymus lyra*.

Of the foraging habits of the Raiidæ little is known. It is nevertheless certain that they depend upon " scent "—or at any rate on some sense other than sight—for the finding and recognition of their food or prey. For in long-line fishing, where the catch depends upon the fish finding and taking the bait, there is no difference at all in the magnitude of day and night hauls. Neither the brightest day nor the darkest night appreciably affects the catches of Ray. They thus differ markedly from Turbot which, being sight feeders, are seldom caught in any number on lines during the night, but are readily taken by day (*vide* appendix, pp. 28–33 *infra*).

VIII. The Toll of the Fishery.

Further work on the Rays and Skates of the Channel Area is proceeding with a view to ascertaining, if possible, their growth-rate and of discovering some method of age determination. Only when more precise information is forthcoming on these points can any definite estimate be made of the toll of the fishery. It seems worth while, nevertheless, to mention here certain facts concerning the fishery which appear to point very definitely to a possible depletion of the stock if the present intensity of fishing continues.

The statistics at present available show an alarming decline in the total British catches of Rays and Skates from the English Channel as a whole during the last five years, the total landings from regions VII d and e (Channel) in the years 1926–1930 being 64,061 cwt., 57,344 cwt., 54,238 cwt., 50,771 cwt., and 45,037 cwt. respectively. Certain factors external to the fishery itself have, in some years at least, helped to cause this decline. But that these figures reflect a real change in the available stock of fish is indicated by events and conditions in the Cornish long-line fishery, according to the following statement by the fishermen concerning the number of hooks used and the grounds fished.

Whereas in pre-war and the immediate post-war years the Cornish long-line fleet working from Newlyn used on an average from 1000 to 1500 hooks per vessel on from $2\frac{1}{2}$ to 3 miles of lines, they now shoot from 2000 to 3000 hooks on from 5 to 7 miles of lines in order to capture approximately the same amount of fish. Moreover, instead of fishing as a rule within a radius of 50 miles from port, they are now obliged, in spite of the inadequacy of their vessels, to seek grounds up to 90 or even 100 miles distant.

As increase in the amount of gear that can be used has now attained its maximum for the type of vessel at present employed in the line fishery, and as there is a limit (now reached) to the distance from port at which they can profitably and safely work, it would appear that the landings must in future decline. It is doubtful whether the use of larger vessels capable of working more gear and of going farther away from port would arrest the possibility of this decline more than temporarily.

It seems sufficiently interesting and important finally to mention that, in line fishing, there is a complete absence of any destruction of nonmarketable small fish.* Should the question ever arise in a restricted area of devising means for the preservation of a Ray fishery, a useful preliminary step would be to consider the possibility of substituting lining for other more destructive methods of fishing.

IX. Acknowledgments.

In carrying out these investigations I have received assistance from so many persons—fishermen, salesmen, buyers, and others—that it is impossible for me here to mention them all individually. Without their aid I could not have worked. To all those, therefore, to whom I am indebted in any way for help and advice I gladly extend my thanks. I am especially grateful to Messrs. Howard and Ben Dunn for much assistance generously given throughout the whole course of the investigations.

I am also under particular obligation to Mr. E. Ford for many valuable suggestions, and for reading the manuscript before it was submitted for publication.

X. SUMMARY.

1. Until the beginning of the present century there was little demand in this country for Rays and Skates. This fishery is now of major importance both nationally and within the Devon and Cornwall area.

2. Of the eleven species of Raia present in the western area of the Channel, *R. clavata* makes the greatest numerical contribution (37%) to the total landings in Devon and Cornwall. The composition of the catches obtained by different methods of fishing varies greatly.

3. *R. clavata* is the most widely distributed species in the Channel area at all depths and on all kinds of sea bottom.

4. In a series of trawl hauls off the west coast of Ireland *R. clavata* was most numerous in the catches down to about 100 fm. From that depth down to about 170 fm. (the greatest depth fished) *R. fullonica* was most numerous.

5. Unispecific and even unisexual shoals of at least three species of Raia—*R. clavata, R. brachyura, R. fullonica*—occur.

6. When more than one species of Raia is present within the same area at the same time, the members of the different species have been found not to mix indiscriminately.

7. *R. clavata* appears to hatch out in shallow water close inshore and gradually move seawards into deeper water as it grows.

* The smallest Ray taken in the three shots recorded on pp. 30–33 (appendix) was a *R. nævus* 33 cm. (about 13 inches) in width across the disc.

8. Adult *R. clavata* show definite migratory movements, though the full extent of their wanderings is not yet known. There is an inshore migration in early spring of adult fish to a small part of the coast near Plymouth. The first fish to appear are females, males appearing later.

9. There is evidence of somewhat similar migratory movements by *R. brachyura*.

10. *R. clavata*—and possibly also *R. brachyura* and *R. batis*—at times may feed almost entirely on Herrings.

11. Large *R. batis* feed to no inconsiderable extent on other species of Raia.

12. In foraging for their food Rays and Skates depend upon some sense other than sight.

13. There has been in recent years a steady decline in the landings of Rays and Skates from the English Channel—probably due to depletion of the available stock of fish.

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XII. APPENDIX.

Below are shown in detail the complete catches of fish, and their distribution on the hooks, taken in three hauls of long-line worked from a Newlyn (Cornwall) motor liner on 22nd and 23rd July, 1931. The interval between adjacent snoods, each of which carried a single hook, was approximately eleven feet.

The various species of fish captured are denoted by the following

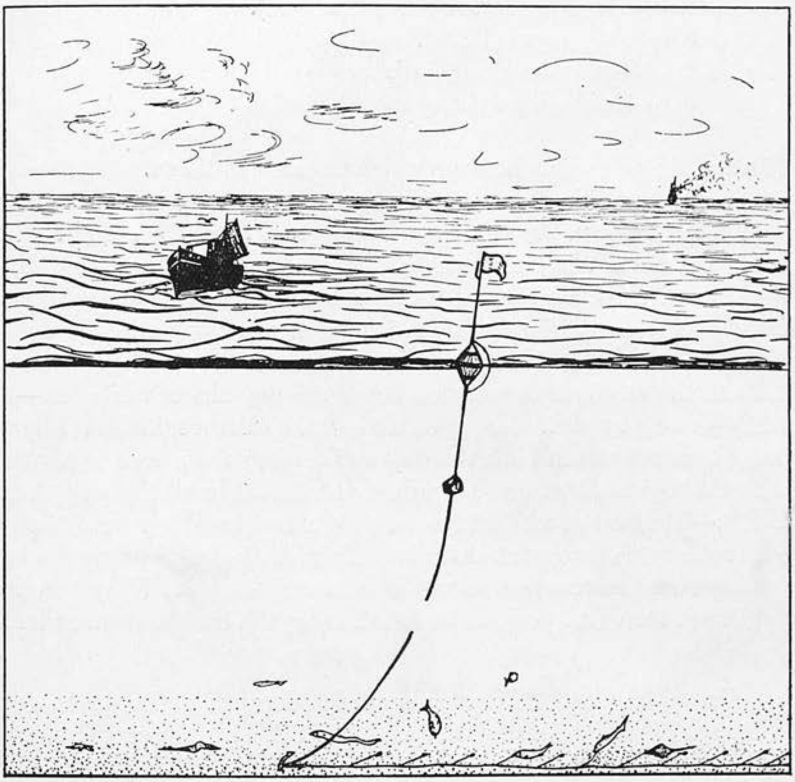

FIG. 6.—Diagram of a Cornish motor liner, and a portion of its long-line which has just been shot. The complete line carries approximately 2600 hooks and extends for a distance of between 5 and 6 miles along the sea floor. For further explanation, see text, p. 30.

symbols in which all *Rays* are indicated by letters and other species by numbers.

C = *Raia clavata* (Thornback Ray).
M = *Raia montagui* (Spotted Smoothback Ray).
N = *Raia nævus* (Cuckoo Ray).
R = *Raia circularis* (Sand Ray).
F = *Raia fullonica* (Shagreen Ray ; Owl Ray).
B = *Raia batis* (Common Skate).

1 = *Acanthias vulgaris* (Spur Dogfish).
2 = *Scyllium canicula* (Rough Dogfish).
3 = *Scyllium catulus* (Nursehound).

4 = *Rhombus maximus* (Turbot).
5 = *Conger vulgaris* (Conger Eel).
6 = *Molva vulgaris* (Ling).
7 = *Trigla gurnardus* (Grey Gurnard).
8 = *Trigla lyra* (Piper).
9 = *Gadus morrhua* (Cod).
0 = *Luidia sarsi* (Long-armed Starfish).

Every dot represents a hook on which no fish was taken.

A record of the blank hooks and fishes caught on the portion of line shown in Figure 6, p. 29, would read as follows : . . . 9 . 1 F . . . .

Here and there along the length of a line small sections frequently become tangled. Such tangled portions have not been recorded in the present census as the hooks which they carry are put entirely out of action as far as their fishing capacity is concerned.

Two of the three shots recorded below are day shots, while one—the second—is a night shot. It will be noticed that Turbot (indicated by the figure 4) are present in both the day catches but that none were taken during the night. Rays and Dogfish are abundant in all three catches.

NOTE.—The first catch here recorded was not considered satisfactory by the fishermen on account of the scarcity of *Raia clavata* (Thornback)—the most remunerative species which is mainly sought. They therefore moved from their first position before shooting the lines a second time.

First Shot. 80 miles S.S.W. of Mousehole (Cornwall). Began to shoot lines 4.30 p.m. ; finished 6.5 p.m. Shot S.W. (24 baskets). Began hauling 8.30 p.m. ; finished 2.15 a.m.. 22nd–23rd July, 1931.

.......................2..1...................1 F ....1...M
.....M.M..1..F...6...1.M....1.....1........4.......C....
.........................1..1.1....1.10.1.......1122........
.......1.......111....0.1....1.N..1.0.M.1..M...1....1...11
...1.N.0.............1.......4.....N.N.M........1..M...
........R.1..1..N..........1...............F......1...N
.....N.1....1.1.................1.....1..1........1.........
..............N....................1.1....C1...1..1N..........
.........1..1..1....................N..........1.....N.......
CR.1.1..M.4M.N......11.........11...........1....1......
11.1.............1..0...N..1....1......1..1...................
.....4.N.1.1....1....11.C..11..1...1......11..1.1...M.....
........B.......116....1..M.1..1......N.N....1..1C..1
.....M............1..........1F....1......1....1.....1....1..
......1...........1...0.0......1.......1.......1...........40...

. . . . B . .0 1. . M . . . . 1 . . . . . 1 0. C 1 F . . .1 . . . .
1.1.1 1. . . .1 1 1. .0. . . . . . . .1. B .1. . N . . . . .1 1 1 1. .1. .1. . . N . . . . B
C . . . . C . . . . N . . . . R . . . .1 1. . . . . M . .
. . . . . .1.1. C 1 1 1. . . . N . . . . .1 1. . . . . . C . . . . . .1 N 1. . . . N 1
. . . N . . C . . . . .1. . . . . .1. . . . . . .1 1. .1. .1 1. . . .
. . . . . N . . . . N . . . . . .1. .1. . . . . .1. . . . . F . M 1 1. . . . .1. . M . C 0.1
. . . . .1. . . .C . . .1. . C . N .1 C . . . . .1. . .1. . . . . .C N.0. . . .
1. . . F . . M 1.1. .1. . . .1.1. N .1.1. . . . .1 C .1. . M .1. M .1. . .1.1. . .
. . . . .1. . . . .1. N . . . . .N. .1.1.1. . . . . .1.M.1. . . . . . .1.1
. .1. N . .1. . . M . . . . R N1. . . . N .1. . . . . . . .1.2. . . . . .2 N. . .1. .
1. . . . . . M . . . . .1. . . . . . . .1. . . . . N . . . . .1. .1.N.
1 N 1. M . . . . .1.1 N .1 N . . . . N .1.1. . . . . .1. . . .1. . . . . . .
1. . . . . .1. . . . . .0 1 1 1. . . . . N . . .1 1. . . . . .1. .1. .1 1 C. .
N .1. . . .1.1. . . . . .1. .1. . . .1. . F . . . .1. .1. . .1. . . . F . .1.1. . . . . . .
. . N . . . . .1.1. . N . . . . F . . . .1. . . . .1. R 1. .1. . . . . . .1.
0. . . . .1 4 B. . .1. .2.1. . .1. .1. N . .2. . . . . .1 1 1. .1. 1
. . . . .1. .1.1.1 1 M . . . . . N . .1.1. . . . . . . .1.1.1 6. . . . . .1.
1 1. C . . C . . . . . .1. .1 1. .1. .1. .2. . . . . . . .1. N .2. . . B . . . . C . .1. N . .
. . . . C .1.1. . . . . . .1 M . .1. . . . . .1. . . . . . C . . . .
. .1.1. .1. . . . . .1.1.1. . . . . .1. . . . . . . .0. . .1. . . .1. . .1. . . . C 0 6. . . . .1. . .
. . . . .1.1. . .1. . .1. . . . . M .1. . . . . . . N .1. . . . . .1 1. . .1. . . . .
. .1 1. . .1. . . . . . N . . . .1. . . . . .1. . M .1.1. . N . . . . .1.1 1 1. .1. . . .
. . . . .1.1. . . . . .1. . . . . F . . . R 1 1 1. M
. . . .1. . .1. M .6. . . .1 0 1. . . . . .1.1. . . . . . R . . . .
. . . . .1. . . .2. . N . . . . . . .1. . .1. .1. F R 1. .2. . . . .0. . . . B . R . .1. . . . . .
B . . . . F . R . . . . .1. . . . . F . . .1 1 1. . . .1 1. . .1 1.1. . . .
1. . . . . .1. .1 C 1. . .1. F . . R 1. .1. .1. . M N . . . . .
. . . . .1. . . . . .1. N . . . . .1 1 1.1. . . .2 1 B
. . . . M M . . . . C .2. . . .1. . . . . . .
11. . . . . . . .1. .1. . . . . C1.1. . . . . .1. . . . .1. . .11.
1. . . . . .1. . .1. . . . . .1. . . . . .

Second Shot. "Steamed" 8 miles S.S.W. from previous berth. Began shooting 3.30 a.m.; finished 4.50 a.m. Shot S.W. (24 baskets). Began hauling 6.15 a.m.; finished 11.10 a.m. 23rd July, 1931.

. . . . N C .1. . . N . . . R . . . . .1 6. . . . .1. . . . .
. . . .1 N . . . . . .6. .1. . . . . N . . . . R . . . . . .1 1.1. .1. . . . R . . . C
. . . . N .1. . . . . . .1 1. . . . . .1. . . . . . M . . . . N . C .1. . . . .
. . . . .C . . . . .0 1. . . . . . M C . . . . .CN. . . . .C. . .M. . .
. .1 1. . . . . .1. . . . . C . . . . . .1. . . . .1. N . . .1. . . . . .C . .M.
1. M . . . . .1. .6. . . . . N 1.1.1. . M . . . . M . . . . 2 . . . .
. . . . .1. . .5. . . . .1.2. . . . . .1. N . . . . .1 1. . . .1. . . .

1C.1......1...C..R..........FC.......N1.11.......6.......
1......5......C..................C...................1....N.....1
..C.C......CC1....1..C.1....1.1...C...1..C..N..........
...C.....C.5..C.M.B1.......C..6.......6....5.6....6.6...
..66..5..55..1CC..1.......6...............1.6CB..C...1..1
...6........1CC.6.5.....N.C5..M......................C.1
...........1.1........6......R.....C..........2..21..........
......1..1.0.....N.N...C1.C...BB2.1..2.51..9N..N.....
......C....2.1.1...15..N.M121........51..C...11.N....
NC..........11....C....11.......10.....C.......1.......C
.....C.....M..0.6M1.........2....C1.....1.1........6...11
.....1NN....6......1N..2.1.1......10....3.......111....1...
.......1....1.1.....................0.C..1........B.11..2C0.2.1.
C......2.................1..F16...1..C1....C.2...C....C.
B..C.1..1....1........10.......1....1........1C...N.......1
.....11......M.....N..1..11.N..........C...C1N12..C...
C...1.1C.....2.1..........C.............M........C..2C..
C......5....0...2CC..B..2....1.C...6.................N.....
1.. C ...... C ....
........1....6...... C ....2FM.........6..
51...C..N6..C..6C.1..........C.............B..N2..C..
.........11.............................1....C6...113..........
.......C1.....C....C.B................C.............C.......
.........................6.C...1F.....21......................1
.......1.6....0..1.........1..........1....1.C.....1.....CF...
..1...........C.........1...6......C.........B....1.....C.N1
F....1NC11...1.0......1........7.1..N.................1.1.....
C.....1..C...2...........N.............1..C.3....C.M....
...1N..........0.BN.....C2......6...........................1
...C..........C1..1.......1..1.11...CM....C.1.C.......N
1B...B.N.......N...11.....1.C..........11.1.101..........
.........C.C.C.....1..6...N.F...1......1......M......C
.....M11.1.....1..........1B.NF.66..1M.1...1.......M...
.....2......N...11.1...B.........1..........0.C1............
...N.1.......N....2.....C.1..1..........11..N.........C.N

Third Shot. Same berth as No. 2. Began shooting 11.20 a.m.; finished 12.15 p.m. Shot N.E. (18 baskets only). Began hauling 2.00 p.m.; finished 6.15 p.m. 23rd July, 1931.

...1............4....4............4.........4...............4......
..4.....................0.................4..4..........4.....4.F
..C............M...........N.............1......N..........

.............0.....................4. C ....

N N C .... M ....0.....4............4...0...

.........0 4........1.............4.........................

........0.. M .1... F 1.... M ....1......4........1......

... N .... F ... N .. M ......1.... C 4.............

......1...........................M ....1..........1...

..0..........5.......2...........N N 0........1............

......4.. C ....4 4 0. F ..0.................M ....4...1..

M 0..0 4...........N .1.............N ......N ....

.......N ....1............1.............R M .1............

1.........1 N ....0..............1...1..................

... N ...... N ... N 8....1.....6.2..1... N .1....1.1...0........

F .. C ....

................................2......1......2..............

... C ...1..... M ....M ....1..1

....1.....0.... C . C ....C ......1... F ....1.0.....1...C....

..1.. C .. M ......1.... C .1.........N . C ....

.........1...............1......0......N .....N .. N N N .....

......1........ C F .0.............1.......4. C .1........... C ..

.......................1.........C ....C ......C....1......

1. C C N .4...... C 1.. N ....1.......1...1... N ....1 C ..4..

11...1..1....4.. N C C C . C ..11... C ..0 C 1...1. C.4 N ..... C...

M ...... C 1. C . C .. C ...... C ..... N ...... F M 1.1 0 1..........

..1.1.........1.....1 C ....1.............1....1.1....0.....

.........1..1....1.......11...0.....11..1....1............1.....

1..1. C .1.........0.1...1 1....1 N .... M 1...1 M ... N 4

........1......1. C ....2.... M ..1... M ....1......1.C...

1.........1 ..1 C 0....4 1........M 4 M ...... C ...1 0 C.... F ....

....1 1.0.... C..1.....1.............4 1.1..........

Rays and Skates of Devon and Cornwall. III. The Proportions of the Sexes in Nature and in Commercial Landings, and their Significance to the Fishery.

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With 1 Figure in the Text.

Introduction.

The belief for long was held by early investigators that among most if not among all Elasmobranch fishes the number of females in the stocks exceeded that of the males. As long ago as 1884 Day (**4**, p. 345) remarked concerning the Thornback Ray, *Raia clavata*, " It has been said that the number of females is in excess of that of the males." Haacke (**9**, p. 246), writing in 1885, says of the Sharks and Rays which he had observed in South Australian waters, " Bei den südaustralischen Haien und Rochen, auf deren Fang ich zu wiederholten Malen ausgezogen bin und von denen mir auch nicht selten Exemplare für das Adelaider Museum zugeschickt wurden, habe ich die Wahrnehmung gemacht, dass Männchen verhältnismässig sehr selten gefangen werden. Ob diese Wahrnehmung auch anderswo gemacht worden ist, weiss ich nicht, jedoch ist es nicht unwahrscheinlich ; in der mir zu Gebote stehenden Litteratur finde ich nichts darüber. Die seltenheit der geschlechtsreifen Männchen, soweit sie sich wenigstens durch die Fangresultate dokumentiert, gilt für sämtliche Species der ziemlich artenreichen südaustralischen Selachierfauna."

In the year 1890 Fulton (**7**, p. 350) made the surprisingly definite statement that " among skates and rays females are in excess ; the ratio being 175 females to 100 males. The observations were mainly made on the thornback ray (*Raia clavata*), but also on the starry ray (*Raia radiata*) and grey skate (*Raia batis*). The females specially preponderate in the latter species." By 1903, however, Fulton had acquired additional data which seem to have caused him to be less certain of the exact numerical ratio of the sexes among these fishes, for in that year, after recording separately his data for each species, he wrote more guardedly as follows : " It will be observed that in no case do the males exceed the females in number, and that with the exception of the shagreen ray,* where the

* Only 8 specimens were examined—4 males and 4 females.

numbers are probably too small to indicate the real proportion, the females are in excess. The amount of excess, however, varies. There is almost equality in the case of the common skate,* while with the thornback, the starry ray, and the sandy ray—although here the figures are small—the excess of females is very considerable."

Lamont (**11**, p. 78) records the proportions of the sexes among Rays and Skates received for dissection at the Zoology Department of Edinburgh University during the four academic years 1921–25. She points out that, so far as she could ascertain, only one source of error might possibly have affected her counts in such a way as to cause them to give an inaccurate picture of the true state of affairs in nature : i.e. that in very immature male specimens the claspers are so small as to be very easily hidden by the pelvic fins, and hence, if they were overlooked, some males might have been recorded as females. It is but little likely, however, that a careful worker would fail to observe the claspers in even the most immature specimens likely to be met with in the dissecting-room.

The numbers† dealt with are small and it seems unnecessary to reproduce them here. It is enough to point out that Lamont found the combined totals for all five species (*R. clavata*, *R. radiata*, *R. fullonica*, *R. circularis*, *R. batis*) which passed through her hands to " show a slight excess of males over females, but this excess was not maintained by each species when considered separately. The excess of males was most marked in *batis*, and was also considerable in *circularis*, but in *clavata* and *fullonica* the condition was reversed and there was a still greater disparity in numbers in favour of the female sex." The results for *R. radiata*, this author points out, call for special remark " because in the last year the occurrence of a great excess of females entirely upset the ratios established for that species during the previous three years." Lamont finally came to the conclusion that while her data " undoubtedly indicate that in the early stages of *batis* males are most numerous, they also appear to provide some justification for the conclusion that in the early stages of *radiata* the opposite is the case and females predominate." She was unable, however, to correlate the great preponderance of females during 1924–25 with any unusual degree of immaturity in the fish of that species dealt with throughout the session. Not only so ; the records obtained for *R. radiata* in that year caused her to modify her " opinion formed at the end of the third year to the effect that in adult *radiata* males come to outnumber the females."

Craigie (**3**, p. 492), from data preserved in the files of the Atlantic Biological Station, St. Andrews, N.B., Canada, found that among four species of Raia represented in the records, all showed a predominance

* Common Skate = Grey Skate already referred to above. Compare the two statements.
† A total of 757 males and 727 females distributed among 5 species.

of females, the percentage of males ranging from 45% in *R. erinacea*, the Tobacco-box Skate, to 35% in *R. lævis*, the Barn-door Skate. This author then proceeds to point out that an abnormal sex ratio having been found in any fish (a 50/50 ratio being considered normal) it is then necessary to find out the cause. This, however—apart from tabulating some highly theoretical possibilities such as differential fertilisation, differential mortality of gametes, differential mortality of zygotes, the conversion of an X- into a Y-chromosome or *vice versa*, etc., he does not himself make any endeavour to do but "attempts merely to make a general survey of available data in order to find out in what cases among Canadian marine fishes there is a problem of abnormal sex-ratio awaiting study."

The above is a brief résumé of all the previous work which the present writer has been able to find on the proportions of the sexes in certain of the Raiidæ. It will serve to show that although there is some evidence which seems to suggest that as a general rule females tend to outnumber the males, such evidence is by no means conclusive, and that there remains yet much to be learned.

Ford (**5**, p. 483), however, in the course of researches on the life-history of the Spur Dogfish (*Acanthias vulgaris*) found that his data concerning the proportions of the sexes in that Elasmobranch also showed a decided preponderance of females in a total of 3022 fish from 13 samples drawn from commercial landings caught over a period of seven months, there being 1947 females and 975 males. At the same time he found that, among large numbers of embryos obtained *ex utero*, males and females were represented in approximately equal numbers, and therefore presumably would have been born in equal numbers, for the embryos in which the sex could be determined must have been all at such a stage of development that differential mortality would be but little likely to supervene before birth.

Now although a differential mortality of gametes or of zygotes is known to occur in some animals and operates to produce an excess of one sex or of the other, that explanation, in view of Ford's results, obviously does not apply to the Spur Dogfish. A differential survival of the young is a factor which might operate after birth to produce an unbalanced sex ratio. Apart from the fact that there is no evidence to suggest that such a factor is operative, it need not seriously be considered because a much more satisfactory explanation has already been put forward. It has been shown by Ford (**5**, p. 484) and confirmed by Hickling (**10**, p. 537) that there is a very definite segregation of these fish according to age and state of sexual development. The latter author has further shown that normally the males are present in shallower water than the females of the same size and that therefore, owing to the strict segregation of both sexes by size and the smaller size attained by the males, in deeper water females predominate. These large females are mostly pregnant and migrate from deep to shallow water to bear their young. "It is therefore," says Hickling, "hardly possible to speak of the sex ratio among dogfishes as if that were a constant; it will clearly vary with depth and also, almost certainly, with season." It is obvious, too, that such differences of habit exhibited by the male and female fish will render them liable in different degree to capture. As the males, though produced in numbers equal to those of the females, are taken less frequently and in smaller numbers than the latter, it is evident that the habits of the females render them the more accessible and/or vulnerable to the usual fishing implements.

The observations of Haacke (*op. cit.*) in Australian waters point to exactly the same conclusion with regard to the Elasmobranch species observed by him in that region. Of the shark, *Mustelus antarcticus*, though females were common, he had never seen a male specimen. Yet when 22 embryos which he was able to obtain were examined they yielded no less than 13 males. Similarly, nearly every adult specimen of *Trygonorhina fasciata* which Haacke encountered was a female. Nevertheless, out of 26 embryos which he examined 15 were males. Of *Rhinobates vincentianus*, a somewhat rare fish, this author had seen but 6 adults, of which only one was a male. But he was able to obtain from 2 of the 5 females which came into his possession 30 embryos—from the one 5 males and 12 females and from the other 10 males and 3 females.

"Es wird interessant sein," continues Haacke, "noch weitere und genauere auf unseren Gegenstand bezügliche, statistische Angaben auch für andere Arten zu sammeln und womöglich die Ursachen der scheinbaren oder wirklichen Minderzahl der geschlechtsreifen Selachiermännchen aufzuklären. Ob die erwachsenen Männchen nicht so leicht an die Angel gehen wie die Weibchen, oder ob viele davon von anderen Männchen ihrer Art im 'Kampf um die Ehe' getötet werden, oder ob endlich junge Männchen einer grösseren Sterblichkeit ausgesetzt sind, vermag ich nicht zu sagen." The most probable explanation almost certainly is that there is some sort of segregation of the sexes amongst the adult fish and that the shoals of males and females exhibit such differences of habit and/or distribution that the former are very much less exposed to capture than the latter.

Results of Plymouth Investigations.

In order to glean some further information on the vexed question of the proportions of the sexes in the British Raiidæ the writer, in the course of his work among these fishes, recorded whenever possible the numbers of the sexes in the samples examined by him. These samples have been drawn from commercial landings by steam, motor, and sailing trawlers by long liners, and by small vessels fishing with set nets, in addition to landings by the Marine Biological Association's research steamer *Salpa*.

In Table III (p. 620) are recorded the numbers of the sexes observed in samples of the seven species most commonly taken in smaller or larger numbers in the English Channel and for which the data are therefore most adequate. Both the actual numbers and the percentages of the sexes have been recorded separately for each sample, irrespective of mode of capture. Two records opposite one date mean that the samples examined on that day were drawn from two separate landings by different vessels. In order to facilitate interpretation an additional column is inserted in which an excess of males in a catch is indicated by an M and excess of females by an F, while the symbol = indicates that the sexes were equally represented. It will at once be seen on referring to this table that females are considerably in excess of the males both in actual numbers and in the number of samples in which they predominate. This applies to all the seven species. But further examination of the figures for individual samples reveals that there is absolutely no constancy in the proportions of the sexes in the different catches of any species. The proportions vary within wide limits. If reference now be made to Table II, which records the landings* from a very specialised local fishery, or to Figure 1 in which the results are graphically represented, this variation will be found there to vary from 100% females to 100% males. It should here be noted that all these landings came from exactly the same very restricted fishing ground (*vide* **12**, p. 6), and were taken with exactly the same fishing gear.

It is practically impossible to determine the proportions of the sexes among our British Rays at or shortly before birth in order to find out how they compare with the conditions found in commercial catches of the adults. All the species are oviparous, and it has not yet been found possible to collect Ray eggs in any number after they have been deposited in the sea so that the developing embryos may be examined for sex. But very recently-hatched individuals of *R. clavata* from about 9 cm. upwards in width of disc have been taken not infrequently by the *Salpa* in her trawl. Of 91 such young individuals of 12·5 cm. and under in width of disc, which have been obtained and their sex recorded, 47 were males and 44 were females. Similar observations on reasonably large numbers of equally young specimens of other species† have not been possible. But interesting and strongly confirmatory data‡ were obtained by observing the proportions of the sexes in 20 out of 21 hauls made by a Plymouth steam trawler during a week's fishing at the mouth of the English Channel

* These figures are not included in Table III.

† Thirty-seven *R. montagui* under 15 cm. in width of disc yielded 17 males and 20 females.

‡ I am indebted to Mr. F. G. Walton Smith, B.Sc., for having collected these data.

TABLE I.

Proportions of the Sexes in Separate Trawl Hauls* taken by a Steam Trawler during one Fishing Trip.

K = fish kept for sale. D = fish discarded as too small.

Date (August, 1932)			19				20		21				22			23	24		
Locality.			Bishop Light bearing E.×S. 30 miles.				Bishop Light bearing E. 50 miles.		Bishop Light bearing E.×S. 30 miles.				Longships Light bearing S.E.×E. 90 miles.			Longships Light bearing S.E.×E. 90 miles.	Wolf Light bearing N. 20 miles.		Totals for each Species.
Duration of Haul (hours)			3½	3½	3½	3½	3	4	3½	3½	3½	3½	3	4	4	4	4	4	
Serial No. of Haul			1	2	3	4	5	6	9	10	11	12	13	15	16	18	20	21	
R. clavata	K	♂♂	–	–	–	1	–	–	–	–	–	–	2	1	4	2	9	5	24
		♀♀	1	–	–	–	1	–	1	–	–	–	–	2	2	1	27	5	40
	D	♂♂	–	1	–	–	1	2	–	–	–	1	–	–	–	–	9	1	15
		♀♀	–	1	–	–	3	–	–	–	–	1	–	–	–	–	6	1	12
R. montagui	K	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	4
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	5	9
	D	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
R. brachyura	K	♂♂	–	3	–	–	–	2	–	–	–	–	–	4	–	–	17	17	43
		♀♀	–	–	–	–	–	–	–	–	1	–	2	7	–	–	25	18	53
	D	♂♂	–	–	–	–	–	1	–	–	–	–	–	–	6	–	4	5	16
		♀♀	–	3	–	–	–	–	–	–	1	–	–	–	2	–	3	2	11
R. nævus	K	♂♂	–	1	–	–	–	–	–	–	–	1	–	1	20	–	10	12	45
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	6	–	7	9	22
	D	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	2	–	3	–	5
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	1	–	4	–	5
R. circularis	K	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		♀♀	1	–	1	1	–	–	3	–	–	1	–	–	1	–	–	–	8
	D	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		♀♀	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
R. fullonica	K	♂♂	3	6	–	4	2	3	12	3	–	11	1	–	–	1	5	2	53
		♀♀	3	3	–	3	1	2	5	3	5	7	2	–	8	2	9	2	55
	D	♂♂	1	1	–	2	–	1	2	–	–	2	–	–	–	–	1	–	10
		♀♀	1	–	–	3	–	–	1	–	–	1	–	–	–	–	1	–	7
R. batis	K	♂♂	1	–	2	1	–	–	–	2	–	–	2	3	6	6	–	–	23
		♀♀	–	1	1	–	–	–	–	–	1	–	–	1	9	4	–	–	17
	D	♂♂	–	1	1	1	–	1	–	1	1	1	1	1	–	2	–	–	11
		♀♀	1	1	1	1	–	–	2	–	–	–	–	–	1	1	–	2	10
R. oxyrhynchus	K	♂♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
		♀♀	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	2
	D	♂♂	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	1	3
		♀♀	–	–	1	–	–	–	1	–	–	–	–	–	1	–	–	–	3

* Haul 8 contained no Rays.
Hauls 7, 14, 19 contained no fish. Trawl torn.
Haul 17 was not recorded.
Haul 3 contained 1 male *R. undulata*—the only specimen taken.

in August, 1932. The data obtained from those fish which were kept for sale and from those which were discarded as being too small to be marketable have been noted separately. All Rays exceeding about 25 cm. in width of disc and Skates of about 35 cm. and over were retained.* The results are summarised in Table I, to which reference should now be made. It will be seen that although in 5 out of the 8 species taken females predominate among the larger retained fish, in not a single instance is this true of the totals for the rejected " smalls." It seems clear, therefore, that in *R. clavata* at any rate, as in *Squalus acanthias*, *Mustelus antarcticus*, *Trygonorhina fasciata*, and *Rhinobates vincentianus*—that is to say, in all the Elasmobranchs in which the embryos or very young fish have been examined for sex—the young are born with the sexes approximately equally represented.† This applies also, almost certainly, to several, if not to all the other Ray species, and possibly to all the Elasmobranchs.

If, then, male and female Rays are born in equal numbers the question arises is there any factor, such as the segregation and shoaling habits found in the Spur Dogfish, which may reasonably be expected to account for the difficulty of obtaining a true picture of the proportions of the sexes in the adults ?

It has already been pointed out briefly by the present writer (**12**, p. 17) that there is ample evidence of sexual segregation among adult Rays of several species and that the same probably is true for all the Channel, if not for all Ray species. Such segregation was first brought forcibly to the writer's notice by the composition of the catches landed on Plymouth market by vessels engaged in fishing for Rays with a kind of fixed net which superficially resembles a trammel but consists of only a single wall and acts simply as a straightforward tangle net. The first of such landings was observed on February 20th, 1930.‡ It will be seen from Table II—in which the entire catches landed by the various boats are recorded separately, each landing opposite one date being the total catch of one vessel—that the earlier landings observed in 1930 consisted almost entirely of female fish. With the approach of March, however, more males appeared and in the last landing recorded there was not a single female present. In the years 1931 and 1932 the landings from the net fishery were examined from the very beginning of the season. It will be

* These sizes are considerably smaller than usual because at the time of this trip fish were very scarce and so nothing was discarded which might add even a little to the total returns for the voyage.

† Clark (**1**, p. 595), however, in the course of investigations on the eggs and young of British Raiidæ, hatched out artificially 23 *R. clavata* of which 15 were females. This is clearly an abnormal ratio (which would probably have been corrected if larger numbers from several fish had been examined—cf. Haacke's results with Rhinobates described on p. 7), for even among the adults a 2 : 1 ratio of females to males does not hold good.

‡ There had been earlier landings but the writer, having had only just taken up the study of the Raiidæ, was until this date quite unaware of the existence of such a fishery.

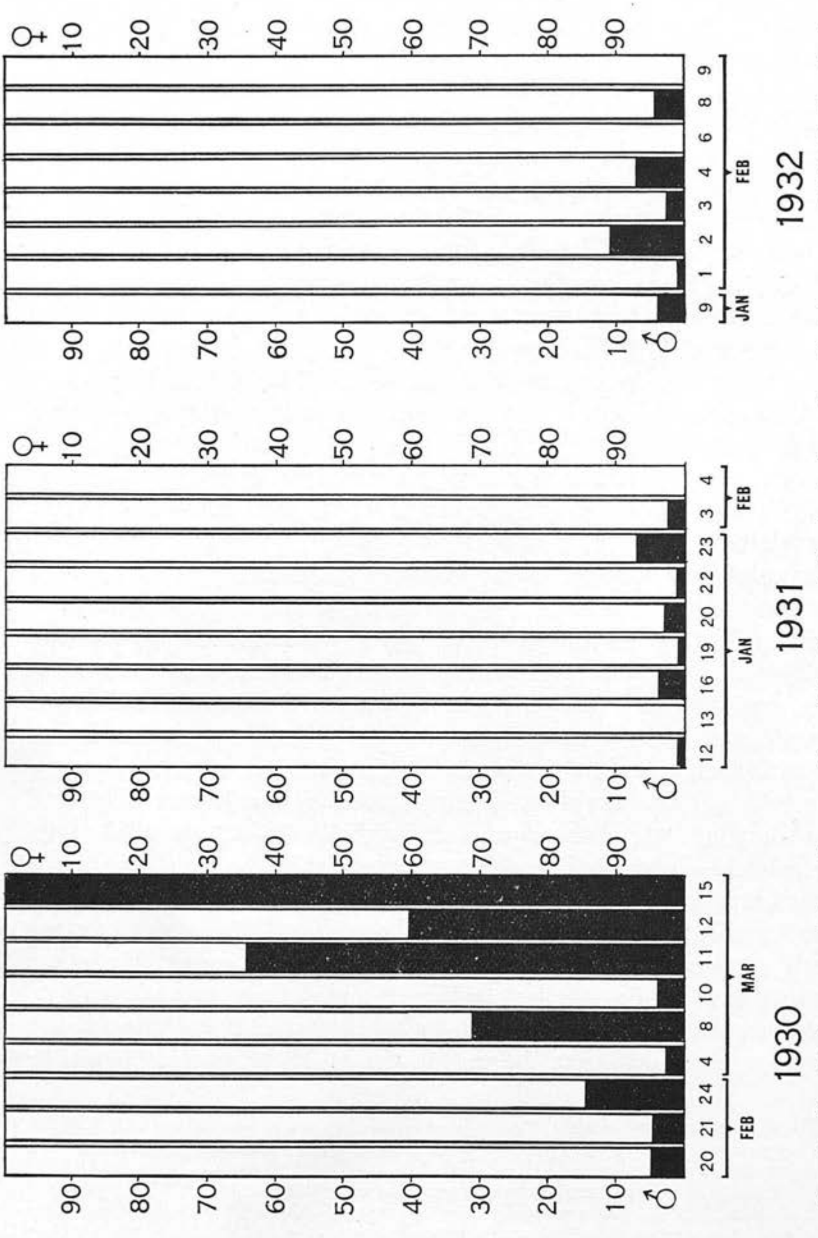

FIG. 1.—Graphical representation of composition of landings of *R. clavata* from Ray Nets in seasons 1930–31–32. Each vertical column represents the *total* landings on one day, the black component being the percentage of male fish and the white component being the percentage of female fish included therein.

TABLE II.

Composition of Landings from Ray Nets—Seasons 1930, 1931, and 1932.

(Not included in Table III, p. 620.)

Date.	Total number of Fish in Landing.	Total ♂♂	Total ♀♀	Percentage ♂♂	Percentage ♀♀
1930.					
February 20	137	7	130	5	95
,, 20	65	3	62	5	95
,, 21	156	7	149	4	96
,, 21	52	3	49	6	94
,, 24	197	21	176	11	89
,, 24	36	13	23	36	64
March 4	34	1	33	3	97
,, 8	26	8	18	31	69
,, 8	38	12	26	32	68
,, 10	35	2	33	6	94
,, 10	14	0	14	0	100
,, 11	104	67	37	64	36
,, 12	69	28	41	41	59
,, 15	38	38	0	100	0
1931.					
January 12	161	2	159	1	99
,, 13	5	0	5	0	100
,, 13	14	0	14	0	100
,, 13	102	0	102	0	100
,, 16	51	2	49	4	96
,, 19	60	0	60	0	100
,, 19	72	0	72	0	100
,, 19	68	2	66	3	97
,, 20	108	3	105	3	97
,, 20	53	2	51	4	96
,, 22	64	1	63	2	98
,, 22	12	0	12	0	100
,, 23	72	9	63	12·5	87·5
,, 23	68	8	60	12	88
February 3	17	1	16	6	94
,, 3	24	0	24	0	100
,, 3	38	1	37	3	97
,, 4	5	0	5	0	100
,, 4	14	0	14	0	100
,, 4	102	0	102	0	100
1932.					
January 9	75	3	72	4	96
February 1	53	1	52	2	98
,, 1	15	0	15	0	100
,, 1	24	0	24	0	100
,, 1	3	0	3	0	100
,, 2	23	0	23	0	100
,, 2	51	8	43	16	84
,, 3	16	0	16	0	100
,, 3	8	0	8	0	100
,, 3	50	2	48	4	96
,, 4	34	4	30	12	88
,, 4	22	1	21	5	95
,, 4	14	0	14	0	100
,, 6	15	0	15	0	100
,, 8	64	8	56	12·5	87·5
,, 8	14	0	14	0	100
,, 8	11	2	9	18	82
,, 8	7	1	6	14	86
,, 9	10	0	10	0	100
,, 9	10	0	10	0	100
,, 9	12	0	12	0	100

Numbers (with percentages) of Males and Females of seven species of Raia included in Samples from Landings from the English Channel—irrespective of Mode of Capture.

Date.		R. clavata.					R. montagui.					R. brachyura.					R. nævus.					R. circularis.					R. fullonica.					R. batis.				
		Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.	Male. No.	Male. %	Female. %	Female. No.	Sex Predominating.
1930																																				
January	15	33	52	48	30	M	9	30	70	21	F	11	42	58	15	F	–	–	–	–		–	–	–	–		12	67	33	6	M	–	–	–	–	
..	16	2	100	–	–	M	24	47	53	27	F	22	38	62	36	F	25	51	49	24	M	–	–	–	–		2	50	50	2	=	–	–	–	–	
..	17	39	62	38	24	M	4	33	67	8	F	5	50	50	5	=	–	–	–	–		3	43	57	4	F	2	33	67	4	F	2	100	–	–	M
..	17	10	40	60	15	F	7	47	53	8	F	–	–	–	–		1	100	–	–	M	–	–	–	–		5	42	58	7	F	1	50	50	1	=
..	20	3	60	40	2	M	23	49	51	22	M	18	53	47	16	M	19	54	46	16	M	–	–	–	–		4	57	43	3	M	–	–	–	–	
..	20	17	42·5	57·5	23	F	17	44	56	22	F	–	–	100	1	F	–	–	–	–		–	–	–	–		1	50	50	1	=	–	–	–		
..	22	12	22	78	43	F	15	60	40	10	M	10	48	52	11	F	–	–	–	–		–	–	–	–		–	–	100	3	F	–	–	–	–	
..	23	11	32	68	23	F	29	48	52	31	F	1	100	–	–	M	17	44	56	22	F	–	–	–	–		2	50	50	2	=	2	50	50	2	=
..	24	10	45	55	12	F	8	44	56	10	F	10	32	68	21	F	–	–	–	–		–	–	–	–		1	100	–	–	M	–	–	–	–	
..	25	10	40	60	15	F	12	43	57	16	F	–	–	–	–		11	46	54	13	F	–	–	–	–		2	25	75	6	F	–	–	100	1	F
..	27	8	44	56	10	F	23	59	41	16	M	4	36	64	7	F	14	82	18	3	M	–	–	–	–		4	40	60	6	F	22	56	44	17	M
..	31	20	61	39	13	M	12	39	61	19	F	–	–	100	1	F	13	30	70	31	F	–	–	–	–		4	50	50	4	=	1	50	50	1	=
February	2	23	62	38	14	M	2	12	88	14	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	3	6	60	40	4	M	8	50	50	8	=	10	40	60	15	F	–	–	100	10	F	–	–	–	–		–	–	100	3	F	–	–	–	–	
..	3	19	56	44	15	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	5	33	43	57	43	F	4	44	56	5	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	11	10	50	50	10	=	11	31	69	24	F	17	30	70	40	F	–	–	–	–		–	–	100	1	F	4	67	33	2	M	–	–	–	–	
..	11	13	57	43	10	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	17	13	46	54	15	F	20	42	58	28	F	15	43	57	20	F	5	31	69	11	F	4	33	67	8	F	3	33	67	6	F	–	–	–	–	
..	17	22	61	39	14	M	13	42	58	18	F	16	42	58	22	F	6	32	68	13	F	–	–	–	–		12	50	50	12	=	3	75	25	1	M
..	17	14	38	62	23	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	27	28	37	63	47	F	3	50	50	3	=	–	–	100	1	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
March	3	17	42·5	57·5	23	F	1	33	67	2	F	–	–	–	–		1	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–	
..	5	10	37	63	17	F	11	44	56	14	F	22	41	59	32	F	3	37·5	62·5	5	F	3	30	70	7	F	6	60	40	4	M	–	–	–	–	
..	7	21	60	40	14	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	12	23	46	54	27	F	19	46	54	22	F	28	42	58	39	F	13	42	58	18	F	–	–	–	–		9	45	55	11	F	3	50	50	3	=
..	16	–	–	100	207	F	–	–	–	–		3	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	19	7	28	72	18	F	11	32	68	23	F	16	40	60	24	F	15	56	44	12	M	4	31	69	9	F	4	36	64	7	F	10	40	60	15	F
April	4	6	55	45	5	M	2	67	33	1	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	10	31	53	47	28	M	1	50	50	1	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	28	6	24	76	19	F	1	100	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
May	6	7	58	42	5	M	2	50	50	2	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	14	25	48	52	27	F	13	39	61	20	F	1	33	67	2	F	12	29	71	30	F	–	–	–	–		3	33	67	6	F	–	–	–	–	
..	21	14	37	63	24	F	6	37·5	62·5	10	F	20	39	61	31	F	–	–	–	–		–	–	–	–		9	35	65	17	F	1	33	67	2	F
..	28	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		41	25	75	125	F
..	29	10	18	82	46	F	–	–	100	2	F	–	–	–	–		2	100	–	–	M	1	14	86	6	F	4	57	43	3	M	–	–	–	–	
..	30	24	44	56	30	F	–	–	–	–		–	–	–	–		1	100	–	–	M	1	14	86	6	F	12	29	71	29	F	–	–	–	–	
..	31	54	39	61	85	F	4	44	56	5	F	–	–	100	2	F	8	57	43	6	M	4	25	75	12	F	19	41	59	27	F	–	–	–	–	
June	2	3	16	84	16	F	1	100	–	–	M	–	–	–	–		2	40	60	3	F	2	50	50	2	=	4	40	60	6	F	–	–	–	–	
..	3	6	43	57	8	F	5	45	55	6	F	–	–	100	1	F	5	42	58	7	F	–	–	–	–		7	64	36	4	M	–	–	–	–	
..	3	2	67	33	1	M	6	60	40	4	M	152	83	17	31	M	–	–	100	9	F	–	–	–	–		–	–	–	–		–	–	–	–	
..	4	–	–	–	–		1	3	97	28	F	469	57	43	355	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	14	99	40	60	147	F	7	47	53	8	F	–	–	–	–		13	28	72	33	F	6	32	68	13	F	90	47	53	102	F	–	–	–	–	

..	17	13	*43*	*57*	17	F	17	*50*	*50*	17	=	8	*36*	*64*	14	F	9	*64*	*36*	5	M	–	–	–	–		4	*44*	*56*	5	F	10	*48*	*52*	11	F
..	21	16	*44*	*56*	20	F	16	*39*	*61*	25	F	19	*43*	*57*	25	F	9	*37·5*	*62·5*	15	F	5	*36*	*64*	9	F	4	*36*	*64*	7	F	–	–	–	–	
August	1	26	*47*	*53*	29	F	14	*54*	*46*	12	M	3	*37·5*	*62·5*	5	F	20	*51*	*49*	19	M	4	*40*	*60*	6	F	–	–	–	–		–	–	–	–	
..	20	15	*36*	*64*	27	F	–	–	–	–		–	–	–	–		33	*35*	*65*	62	F	2	*40*	*60*	3	F	–	–	*100*	3	F	2	*29*	*71*	5	F
..	20	–	–	–	–		–	–	*100*	1	F	1	*1*	*99*	170	F	2	*100*	–	–	M	–	–	–	–		–	–	–	–		–	–	–	–	
..	21	12	*29*	*61*	19	F	3	*37·5*	*62·5*	5	F	–	–	–	–		25	*34*	*66*	49	F	–	–	–	–		3	*60*	*40*	2	M	–	–	–	–	
..	23	–	–	–	–		4	*57*	*43*	3	M	60	*43*	*57*	79	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	23	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	*100*	9	F	–	–	–	–	
November	7	6	*43*	*57*	8	F	15	*52*	*48*	14	M	19	*38*	*62*	31	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	10	14	*42*	*58*	19	F	4	*33*	*67*	8	F	5	*33*	*67*	10	F	–	–	–	–		1	*3*	*67*	2	F	4	*57*	*43*	3	M	1	*50*	*50*	1	=
..	18	31	*42*	*58*	42	F	23	*40*	*60*	34	F	32	*46*	*54*	38	F	14	*58*	*42*	10	M	5	*33*	*67*	10	F	6	*40*	*60*	9	F	2	*50*	*50*	2	=
..	24	17	*39*	*61*	27	F	6	*37·5*	*62·5*	10	F	11	*48*	*52*	12	F	–	–	–	–		–	–	–	–		9	*82*	*18*	2	M	2	*33*	*67*	4	F
..	28	18	*39*	*61*	28	F	11	*58*	*42*	8	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
December	8	24	*50*	*50*	24	=	19	*59*	*41*	13	M	2	*29*	*71*	5	F	15	*44*	*56*	19	F	–	–	–	–		4	*44*	*56*	5	F	–	–	–	–	
..	11	16	*43*	*57*	21	F	22	*52*	*48*	20	M	–	–	*100*	2	F	18	*50*	*50*	18	=	–	–	–	–		6	*50*	*50*	6	=	–	–	–	–	
..	16	22	*71*	*21*	9	M	2	*33*	*67*	4	F	5	*36*	*64*	9	F	–	–	*100*	4	F	–	–	–	–		–	–	–	–		–	–	–	–	
..	22	–	–	*100*	2	F	1	*17*	*83*	5	F	13	*43*	*57*	17	F	–	–	–	–		–	–	–	–		7	*64*	*36*	4	M	–	–	–	–	
1931.																																				
January	8	–	–	*100*	4	F	22	*51*	*49*	21	M	–	–	–	–		11	*37*	*63*	19	F	–	–	*100*	1	F	–	–	–	–		–	–	–	–	
..	16	27	*37·5*	*62·5*	45	F	2	*25*	*75*	6	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	*100*	6	F	1	*50*	*50*	1	=
..	17	14	*48*	*52*	15	F	10	*53*	*47*	9	M	1	*13*	*67*	2	F	–	–	*100*	1	F	–	–	–	–		10	*62·5*	*37·5*	6	M	–	–	–	–	
..	23	1	*33*	*67*	2	F	23	*55*	*45*	19	M	26	*39*	*61*	40	F	33	*59*	*41*	23	M	–	–	–	–		1	*20*	*80*	4	F	–	–	*100*	2	F
February	3	7	*17*	*83*	35	F	14	*52*	*48*	13	M	31	*60*	*40*	21	M	–	–	–	–		–	–	–	–		4	*27*	*73*	11	F	–	–	*100*	4	F
..	5	21	*40*	*60*	32	F	26	*51*	*49*	25	M	–	–	*100*	1	F	–	–	–	–		–	–	–	–		1	*50*	*50*	1	=	–	–	–	–	
..	9	25	*43*	*57*	33	F	30	*49*	*51*	31	F	–	–	–	–		22	*61*	*39*	14	M	–	–	–	–		–	–	–	–		–	–	–	–	
..	13	11	*44*	*56*	14	F	3	*27*	*73*	8	F	–	–	–	–		–	–	–	–		–	–	–	–		5	*42*	*58*	7	F	12	*44*	*56*	15	F
..	16	1	*25*	*75*	3	F	14	*34*	*66*	27	F	11	*44*	*56*	14	F	12	*33*	*67*	24	F	–	–	–	–		4	*31*	*69*	9	F	1	*33*	*67*	2	F
..	21	21	*47*	*53*	24	F	29	*43*	*57*	39	F	1	*100*	–	–	M	29	*66*	*24*	15	M	–	–	–	–		3	*60*	*40*	2	M	–	–	–	–	
..	24	28	*65*	*35*	15	M	7	*24*	*76*	22	F	23	*50*	*50*	23	=	–	–	–	–		–	–	–	–		5	*38*	*62*	8	F	–	–	–	–	
..	26	12	*40*	*60*	18	F	11	*61*	*39*	7	M	–	–	–	–		17	*40*	*60*	26	F	–	–	–	–		–	–	*100*	3	F	1	*50*	*50*	1	=
March	3	14	*47*	*53*	16	F	5	*36*	*64*	9	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	3	–	–	–	–		17	*50*	*50*	17	=	–	–	–	–		16	*46*	*54*	19	F	5	*29*	*71*	12	F	12	*80*	*20*	3	M	2	*50*	*50*	2	=
..	5	18	*53*	*47*	16	M	24	*56*	*44*	19	M	14	*31*	*69*	31	F	–	–	–	–		4	*50*	*50*	4	=	6	*60*	*40*	4	M	5	*28*	*72*	13	F
..	9	2	*40*	*60*	3	F	13	*41*	*59*	19	F	15	*39*	*61*	23	F	7	*24*	*76*	22	F	–	–	–	–		–	–	–	–		2	*33*	*67*	4	F
April	25	16	*43*	*57*	21	F	16	*46*	*54*	19	F	22	*54*	*46*	19	M	–	–	–	–		7	*44*	*56*	9	F	6	*55*	*45*	5	M	–	–	–	–	
..	29	16	*39*	*61*	25	F	10	*48*	*52*	11	F	26	*39*	*61*	41	F	–	–	–	–		–	–	–	–		–	–	–	–		8	*31*	*69*	18	F
May	4	18	*55*	*45*	15	M	4	*14*	*86*	25	F	12	*32*	*68*	26	F	–	–	–	–		12	*52*	*48*	11	M	–	–	–	–		1	*33*	*67*	2	F
..	11	20	*43*	*57*	26	F	27	*45*	*55*	33	F	19	*40*	*60*	28	F	–	–	–	–		–	–	–	–		14	*70*	*30*	6	M	1	*33*	*67*	2	F
..	12	14	*54*	*46*	12	M	3	*50*	*50*	3	=	1	*25*	*75*	3	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	22	21	*47*	*53*	24	F	8	*26*	*74*	23	F	14	*40*	*60*	21	F	–	–	–	–		–	–	–	–		3	*37·5*	*62·5*	5	F	2	*33*	*67*	4	F
..	26	21	*42*	*58*	29	F	15	*48*	*52*	16	F	3	*100*	–	–	M	19	*47·5*	*52·5*	21	F	–	–	–	–		5	*83*	*17*	1	M	–	–	–	–	
June	1	11	*37*	*63*	19	F	2	*40*	*60*	3	F	–	–	–	–		1	*100*	–	–	M	–	–	–	–		9	*69*	*31*	4	M	–	–	–	–	
..	4	29	*45*	*55*	36	F	29	*48*	*52*	31	F	2	*100*	–	–	M	35	*49*	*51*	36	F	–	–	–	–		3	*33*	*67*	6	F	3	*33*	*67*	6	F
..	4	6	*40*	*60*	9	F	11	*50*	*50*	11	=	–	–	–	–		–	–	–	–		–	–	–	–		6	*29*	*71*	15	F	2	*40*	*60*	3	F
..	8	5	*42*	*58*	7	F	10	*62·5*	*37·5*	6	M	11	*34*	*66*	21	F	19	*49*	*51*	20	F	–	–	–	–		15	*47*	*53*	17	F	–	–	–	–	
..	10	27	*44*	*56*	34	F	29	*41*	*59*	41	F	–	–	–	–		3	*30*	*70*	7	F	–	–	–	–		12	*52*	*48*	11	M	1	*33*	*67*	2	F
..	15	20	*48*	*52*	22	F	19	*46*	*54*	22	F	18	*51*	*49*	17	M	–	–	–	–		–	–	–	–		7	*39*	*61*	11	F	–	–	*100*	1	F
..	16	22	*48*	*52*	24	F	26	*50*	*50*	26	=	–	–	*100*	1	F	31	*47*	*53*	35	F	–	–	–	–		10	*48*	*52*	11	F	5	*50*	*50*	5	=
..	23	29	*63*	*37*	17	M	15	*79*	*21*	4	M	23	*38*	*62*	37	F	–	–	–	–		–	–	–	–		3	*43*	*57*	4	F	3	*43*	*57*	4	F
July	3	17	*49*	*51*	18	F	9	*50*	*50*	9	=	15	*65*	*35*	8	M	–	–	–	–		–	–	–	–		4	*57*	*43*	3	M	–	–	*100*	1	F
..	3	16	*67*	*33*	8	M	–	–	*100*	1	F	–	–	–	–		8	*62*	*38*	5	M	–	–	–	–		4	*50*	*50*	4	=	–	–	–	–	
..	13	13	*48*	*52*	14	F	18	*47*	*53*	20	F	27	*47*	*53*	31	F	–	–	–	–		3	*50*	*50*	3	=	3	*43*	*57*	4	F	–	–	–	–	
..	14	17	*57*	*43*	13	M	8	*62*	*38*	5	M	1	*100*	–	–	M	–	–	*100*	9	F	–	–	–	–		–	–	–	–		–	–	–	–	
..	29	26	*15*	*85*	149	F	–	–	–	–		–	–	–	–		12	*63*	*37*	7	M	–	–	*100*	1	F	17	*52*	*48*	16	M	–	–	*100*	1	F
October	10	22	*51*	*49*	21	M	1	*50*	*50*	1	=	7	*70*	*30*	3	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	28	14	*45*	*55*	17	F	4	*50*	*50*	4	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
November	2	–	–	*100*	3	F	2	*50*	*50*	2	=	2	*67*	*33*	1	M	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	27	5	*23*	*77*	17	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
December	2	4	*40*	*60*	6	F	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	15	6	*32*	*68*	13	F	2	*50*	*50*	2	=	–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–		–	–	–	–	
..	23	11	*61*	*39*	7	M	4	*57*	*43*	3	M	–	–	*100*	2	F	–	–				–	–				–	–				–	–	–	–	

seen from the table that few males were present in any landing and that not infrequently an entire catch would consist wholly of female fish. This is not explainable by any selective action of the nets as these were the same at the beginning as at the end of the season in 1930. Nor does it appear to be true that the males are not caught because they exhibit some difference (or absence) of movement. When present they are taken quite as successfully as the females.

There is no doubt, therefore, that on this particular fishing ground, during the first three or four months of the year, the Ray population may consist entirely or almost entirely of one sex of a single species. The composition of this population may change rapidly and completely during the brief season of the net fishery, which is simply the time during which fully adult fish are present on the ground in large numbers. The main population consists first, and for the greater part of the season, of mature females with, in some seasons at least, mature males appearing later and for a shorter time towards the end of the season.* Finally, for the greater part of the year, only a residuum of immature individuals of both sexes is present, the adult fish having migrated elsewhere.

Having discovered such very definite segregation of the sexes of *R. clavata* on the Plymouth net fishing ground, coupled with a definite migratory movement of greater or less extent, the question now arises as to whether or not this is an isolated phenomenon or whether there is evidence of similar segregations and migrations elsewhere and for other species. For the purpose of obtaining true samples of fish stocks fixed nets possess a unique superiority over other fishing implements such as trawls and long-lines in that their fishing action is restricted to one very small patch of ground. Unfortunately the writer is not aware of the existence of any other ray-net fishery such as that carried on from Plymouth at any other point on the coast, at any rate within his range of investigation. Nevertheless, a considerable though less complete body of evidence is available from catches obtained by other methods of fishing.

On the night of Saturday–Sunday, March 15th–16th, 1930, between the hours of 7 p.m. and 2 a.m., a steam trawler fishing in shallow water off the Cornish coast caught 210 large Rays, 207 of them being *R. clavata*, every one of which was a female. Obviously this vessel had fallen upon a shoal of female fish similar to that fished by the nets on the Plymouth grounds. It is not to be expected, however, that such a pure landing will occur in trawl or line fishing except at very rare intervals, because even one haul of a trawl or a fleet of lines once shot samples a large area of the sea floor ; and every landing is the product not of one but of many hauls

* Unfortunately, owing to the onset of unfavourable weather conditions, this fishery was brought to a premature close in both 1931 and 1932, so that it is not known whether or not the males appeared towards the end of the season in those years.

of the trawl or a fleet of lines several if not many times shot. That the landings from both trawlers and liners should, in spite of this, not infrequently consist largely and sometimes almost entirely of one sex of a single species points clearly to the occurrence of sexual segregation among species other than *R. clavata* and on grounds other than that fished by the Plymouth nets. Some of the most striking of such landings recorded by the present writer are enumerated below.

On June 3rd, 1930, a small inshore trawler fishing near Newlyn, Cornwall, brought ashore 205 Rays. Of these no less than 183 were *R. brachyura*, all immature, and containing 152 males. Nine *R. nævus* were included in this catch, every one a female. On the following day a small liner fishing on or near the same ground landed 853 Rays, 824 of which were immature specimens of *R. brachyura*. In this catch, however, males and females were present in more nearly equal numbers, there being 469 males and 355 females. *R. montagui* was the only other species included in the catch. Of these 29 individuals, all were adult fish and consisted of 28 females with only a single male included among them. In August of the same year this liner was still fishing on the same ground, but the *R. brachyura* which she was then landing were all mature fish which must have migrated there (*vide* **12**, p. 23). On August 20th this vessel landed 171 adult Rays of this species of which only one was a male. Three days later another but smaller catch was landed in which adult males and females were almost equally represented, there being 60 of the former and 79 of the latter sex. After this date the writer had to leave Newlyn, otherwise it would have been interesting to have noted whether or not the males eventually exceeded the females in number or even completely "replaced" them as happened in the case of *R. clavata* on the Plymouth net grounds in the spring of the year.

There was another interesting landing on August 23rd. A liner which had been fishing in deep water caught only 9 Rays on its full fleet of lines which had been shot once. All these were *R. fullonica* and all adult females.

On July 29th, 1931, a liner from the same port landed 175 *R. clavata* in addition to small numbers of other species. Of these Thornback Rays 149 were adult females; the 26 males were mostly immature. On May 31st, 1932, a liner's catch was observed to contain 19 *R. marginata*, all females over 100 cm. in width of disc, and all containing ripening ova. On June 2nd another landing contained 39 *R. batis* of which 37 were mature or nearly mature males and 2 were immature females.

In no instance was any information available as to how the fish were distributed on the lines. In the hope that an interesting catch similar to one of those mentioned might be taken in his presence the writer went to sea in a liner and recorded the species and sex of every Ray which came up in the order in which it appeared (*vide* **12**, p. 28). Unfortunately only a very " ordinary " catch rewarded his efforts ; 192 *R. clavata* were taken the majority of which were immature and the two sexes were more or less indiscriminately intermingled all along the line. There was a slight excess of females. The catch of *R. nævus*, the only other species taken in any numbers, was more interesting ; 142 specimens were taken, 104 of which were males, most of them fully adult. The females, of which only an occasional specimen occurred here and there at wide intervals, were found on examination to be mainly immature, only 7 out of the total 38 containing ripe or ripening ova.

Other species were represented by only a very few scattered individuals.

It seems clear, however, from the main body of the evidence brought together in this paper, that the so-called abnormal sex-ratio found among the commercial landings of Rays and Skates is due not to any differential production of males and females at birth, or to a differential mortality after birth, but to differential catches of the sexes owing to segregation of the larger fish into unisexual shoals for at least part of the year. The females, particularly when in a gravid or spawning condition, form more compact schools than do the males, and therefore tend to be captured in greater numbers.

This fact is of much more than theoretical interest ; it has a direct practical bearing on the commercial fishery for these species, which have now become of primary and growing importance as national food fishes. It is well known that for the maintenance of any animal stock the female is, from the numerical point of view, the more important sex. Since, therefore, the females of the Raiidæ as a general rule are captured in considerably greater numbers than the males, it follows that the greatest drain of the fishery upon the fish stock falls upon its most vulnerable part. These Elasmobranch fishes will therefore be much more rapidly and more severely affected by intense fishing in any particular area—such as the English Channel—than species in which there is not an excess of females caught by ordinary fishing methods. Such an effect will tend to be greatly minimised in the case of strongly migratory species—such as the Spur Dogfish, for instance. The stock of such fishes on any particular fishing ground will be exposed to capture only for so long as it remains in that region. Not only so, its numbers will always tend to be sustained or replenished by immigrants from other localities where fishing is less intense or non-existent. It may be highly significant, therefore, that from being a very flourishing concern, the English Channel fishery for Spur Dogfish has, in the course of the last five years, shrunken to almost negligible proportions* owing to the

* The Ministry of Agriculture and Fisheries returns of landings from the English Channel during this period are : 1928, 54,206 cwt. ; 1929, 28,920 cwt. ; 1930, 27,188 cwt. : 1931, 16,049 cwt. ; 1932, figures not yet available.

scarcity of these fish—*and that in spite of their being a pelagic and migratory species.*

On the other hand, the adverse effect of intensive fishing will be correspondingly increased in the case of species—such as the Raiidæ—whose migrations appear to be very restricted or even quite local in character. Moreover, these very same factors which by their action will assist the commercial forces of depletion will be equally potent in retarding recovery once a decline has been brought about in the stocks.

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Observations on the Growth of the Claspers and Cloaca in *Raia clavata* Linnaeus.

By

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With 7 Figures in the Text.

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I. INTRODUCTORY.

In the course of work on the life-history and biology of the Raiidæ in the English Channel, and especially of *R. clavata*, the most important species commercially (**4**, p. 9 *et seq.*), it has been found necessary to attempt to disentangle the migrations of sexually mature fishes from those of juvenile individuals by means of marking experiments. In both sexes sufficiently small individuals could with safety be written down as juveniles and the largest of both sexes as adults. There remained, however, a considerable but ill-defined range of sizes (different in the two sexes) within which might be found fishes of all stages—juveniles, adolescents and adults.

In dealing with male fishes this difficulty was overcome by noting the size and condition of the claspers. In the female, however, the writer was not aware of a corresponding—or any other—external feature from which could be deduced with reasonable accuracy *in a live fish* her state of sexual development. The present investigation was undertaken, therefore, in order to discover whether or not such a feature existed. Attention soon became directed to the greatly accelerated relative growth rate in the cloaca of adolescent fishes and the relatively much greater length of this organ in mature than in juvenile individuals.

During this adolescent period of greatly accelerated growth in length, the cloaca also changes markedly in shape, becoming very much widened out, especially at its inner end (*cf.* Figs. 4 and 5). These changes in the size and shape of the cloaca are so extensive as to be easily discernible by digital examination. There is thus available in the female as well as in the male a ready means of ascertaining the sexual condition of the live fish. This method is now being applied in all further Ray-marking experiments.

The results of detailed observations on these changes in the growth of the claspers and cloaca in *R. clavata* form the substance of this paper.

II. The Claspers.

All species of Rays and Skates (Raiidæ) exhibit well-marked sexual dimorphism. Some of the secondary sexual characters, such as the presence of alar and malar spines and more pointed teeth in the male, become obvious only in sexually mature or nearly mature individuals. The presence of claspers in the male can be detected, however, at a very early stage of development. Thus, during at least the latter part of their embryonic development within the egg, and throughout the entire post-embryonic life of these fishes, the presence or absence of claspers forms a ready means of distinguishing male from female. In addition to their being the most characteristic and most easily discernible feature of the male fish, the claspers serve also, better than any other externally evident character, as an index of his state of sexual development. During the entire period of juvenile growth, before the onset of adolescence,* the claspers remain relatively small and inconspicuous, so much so that they may be entirely invisible from the dorsal side being shorter than, and hidden by, the pelvic fins. But at the onset of adolescence the claspers suddenly begin to grow very rapidly, and their tips soon extend backwards far beyond the limits of the pelvic fins.

This sudden change in the size and condition of the claspers was long ago noticed by ichthyologists. In the year 1877, for example, Malm (**3**, p. 607) stated that in a male *R. clavata* 216 mm. long the claspers were only about 3 mm. in length. In 1895 Fries (**2**, p. 1106) wrote that in a male of this species about 45 cm. long the claspers were " still quite small and short, their tips extending only a little more than half-way along the ventral fins." In a specimen 52 cm. in length he records that the circumstances were " essentially the same " except that the claspers were just a little longer in relation to the fins. But in an individual " rather more than 60 cm. long " Fries remarks that the claspers were so well developed that their tips extended back to more than half-way along the length of the tail.

In order to follow more closely these changes in the relative growth rate

* The post-embryonic life of a Ray is very clearly divided into the usual phases: (1) the *juvenile* phase, during which the fish simply grows in size; (2) the *adolescent* phase, during which fundamental changes take place very rapidly and bring the individual to puberty; (3) the *adult* (sexually mature) phase.

of the claspers, measurements have been made on representative samples of male *R. clavata* at all sizes from recently-hatched individuals upwards to the largest obtainable. In recording the lengths of the claspers, for the sake of uniformity all measurements have been made on the left clasper. The length has been taken as the distance between the tip of the clasper and its point of emergence from the skin on the inner side (Fig. 1). This point is sometimes not well defined in adult fishes with large claspers, and exact measurements are not with them possible. A small part of the variation in recorded clasper lengths of adult fishes must be ascribed,

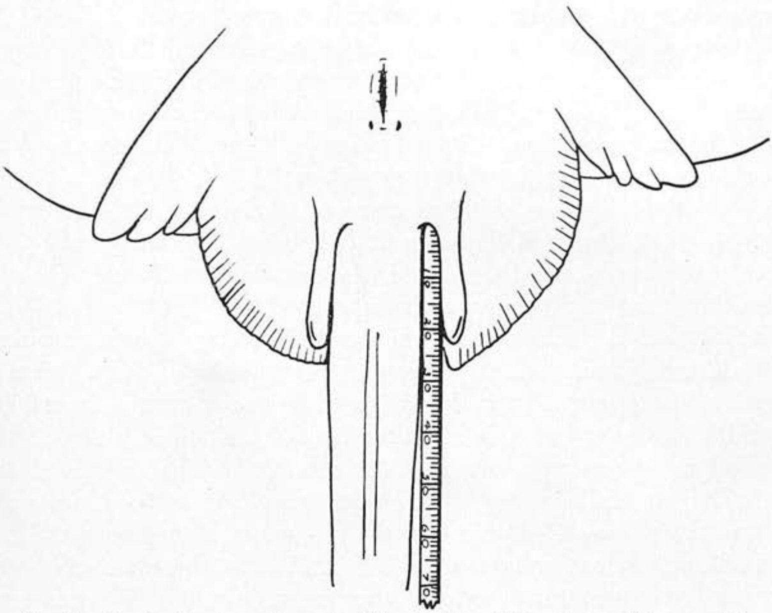

FIG. 1.—*R. clavata*—juvenile male; 31 cm. disc width; clasper 22 mm. $\times \frac{2}{3}$. (See text.)

therefore, to the action of this purely extrinsic factor as well as to the individual variations in size and body-proportions which are always found in the separate representatives of every animal (and plant) species.

It is found that throughout the immature stages of development the claspers grow slowly and regularly, their length at any time during the juvenile phase showing a linear correlation with the total size of the fish, as expressed, say, by width of disc; that is to say that points representing the length of the clasper at different times during the juvenile growth period plotted against the width of the disc fall upon a straight line. This is well shown in Figure 2. Each plotted point indicates the mean value of numerous clasper measurements in centimetre size-groups of fishes. The lengths of the vertical lines drawn through those points indicate the ranges of the measurements from which the means were drawn.*

It will be seen that for fishes up to and including the 43-cm. size-group the mean values lie very closely along the straight line *ab*, the correlation equation for which is

$$Y = 0{\cdot}993\,X - 5{\cdot}596$$

where Y = length of clasper (in mm.), and X = width of disc (in cm.). In succeeding size-groups the ranges of clasper length measurements show progressive extension in an upward direction and the mean values rise rapidly above the line *ab*. This means that in some fishes the claspers are now exhibiting a greatly accelerated relative growth rate.

In size-groups 50 cm. to 54 cm. (inclusive) disc widths, the ranges of clasper lengths reach and retain maximum values, these organs now having attained the fully adult size in some fishes while in others they still remain in the juvenile condition. Examination of Figure 2 clearly shows that the onset of the change in relative growth rate of the claspers, with which are correlated all the other phenomena of adolescence, does not always take place in all fishes at the same size. In some this change takes place when they have attained a disc width of round about 44 cm. ; in others it is delayed until a much larger size is reached.

In Figure 3 these results, for the larger fishes, are shown graphically in a different manner which brings out this point more fully. Here the length of the clasper in individual fishes of 5-cm. size-groups, from 36 cm. in width of disc upwards, is indicated by the position of a dot. In the smallest size-group represented—36–40 cm. disc widths—all the claspers are still short and the range of recorded lengths is small. In the size-group next above—41–45 cm. disc widths—most of the fishes still have short claspers, but a few have entered the adolescent phase and are showing increased relative growth rate of this organ. In the size-group next higher again this process has proceeded still farther and one individual has actually become fully mature.

The size-group 51–55 cm. disc widths is of particular interest. Here the clasper length measurements show two distinct modes—one at the lower end of the range, produced by fishes which are still in the juvenile phase, and one at the upper end of the range, produced by fully adult individuals.† The approximately symmetrical bi-modal curve produced by the clasper length measurements of this group confirms the conclusions to be deduced from analyses of the complete data presented in Figures 2 and 3. These are :—

(1) that, in the English Channel area, in any sample of male *R. clavata*

* Mean values for those size-groups which include adolescents and later stages are without significance and are not shown.

† Shortest clasper found in a fully mature male—176 mm. (*vide* dotted line, Figs. 2 and 3).

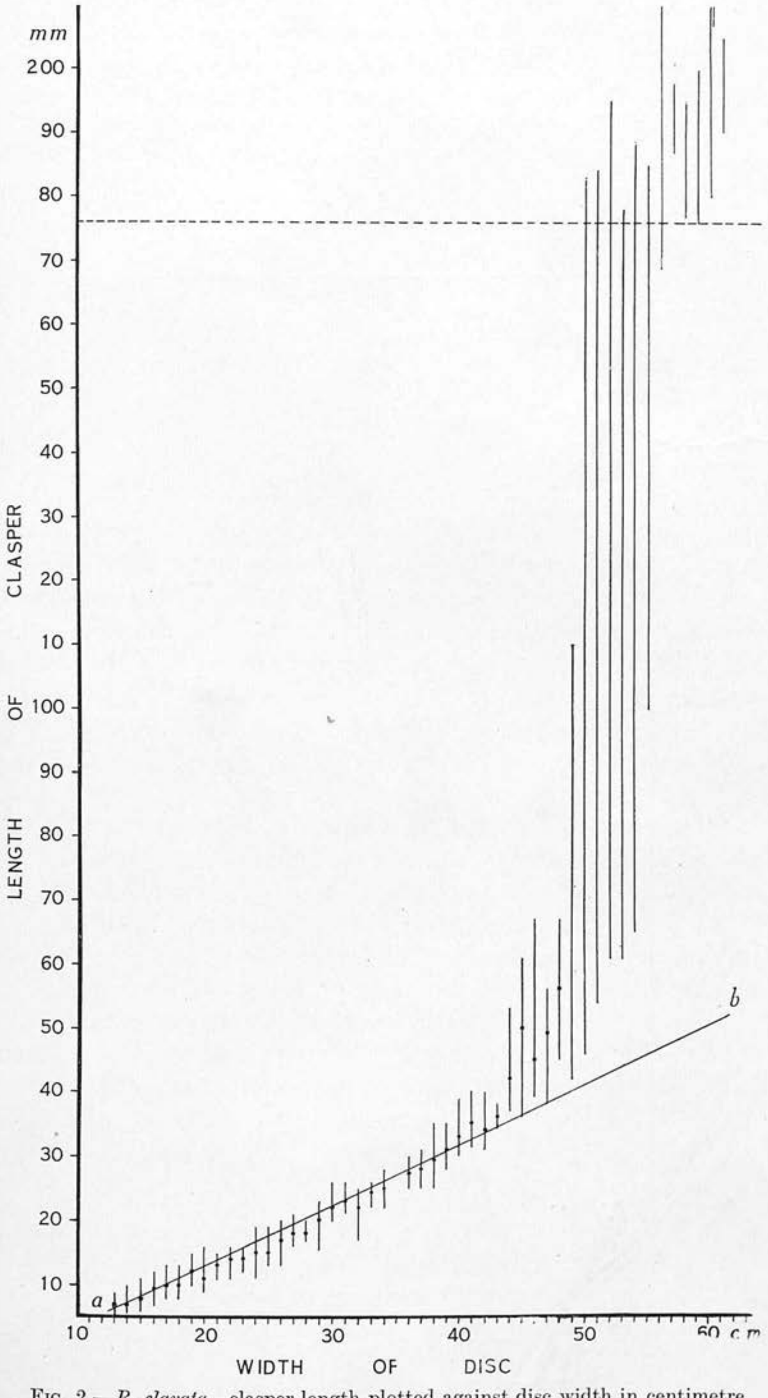

FIG. 2.—*R. clavata*—clasper length plotted against disc width in centimetre size-groups. (For explanation see text p. 889.)

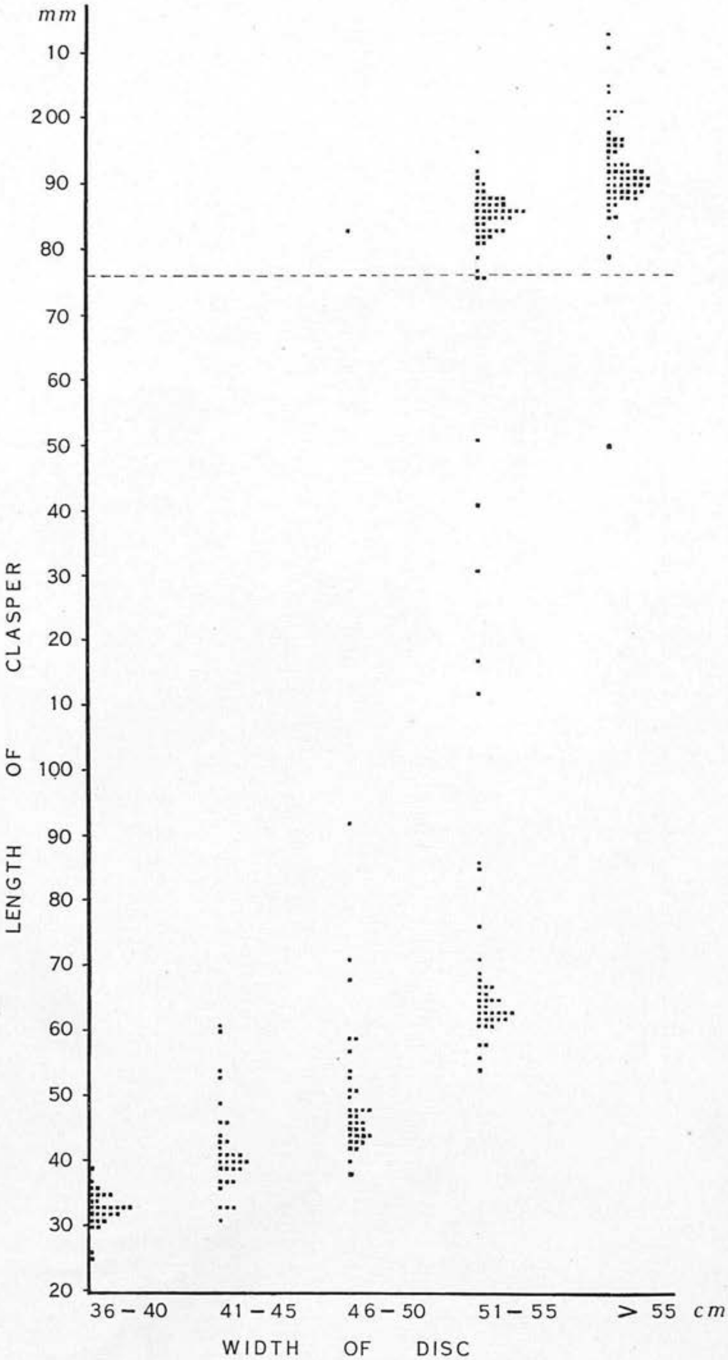

FIG. 3.—*R. clavata*—clasper length plotted against disc width in 5 cm. size-groups. (For explanation see text p. 890.)

in which no fish exceeds about 50 cm. disc width, the great majority of the individuals will be immature juveniles. This will hold true whether the sample be restricted to any arbitrary size-group of small range or consists of fishes at all sizes up to 50 cm. (about) disc width. Over most of this range samples of restricted size-groups will consist of 100 per cent juveniles, but samples at or near its extreme upper limit will contain a certain proportion of individuals at more advanced stages.

(2) that, similarly, in any sample which includes no fishes of less than approximately 56 cm. disc width, the majority of the individuals will be mature adults.

(3) that, in any representative sample of male fish of size-group 51–55 cm. (inclusive) disc widths, juveniles and adults will tend to be equally represented, while adolescents at all intermediate stages will also be found.

III. The Cloaca.

The cloaca of the female Ray exhibits growth phenomena very similar to those found in the claspers of the male, and cloacal measurements have been made on individuals at all stages of growth. The distance from the anterior edge of the cloacal opening to the anterior end of the cloaca (in the middle line) when in normal extension, has been used as the measure of cloacal length. This measurement is made by opening the abdominal cavity and placing the tip of one finger of the left hand against the anterior end of the cloaca as it lies in position. At the same time a not too sharply pointed rod, graduated in millimetres, is inserted into the cloacal aperture and pushed forward until it presses against the left-hand finger. The length of the cloaca is then read off where the anterior edge of the cloacal external opening crosses the rod (Figs. 4 and 5).

Throughout the juvenile phase the cloaca grows only slowly and, like the clasper of the male, preserves a linear correlation between its length and the body dimensions of the whole fish. In Figure 6 the cloaca lengths in fishes of centimetre size-groups are plotted against disc widths. For fishes up to and including the 59-cm. size-group the mean values lie very closely along the straight line *ab* whose correlation equation is

$$Y = 0{\cdot}574\,X - 2{\cdot}175$$

where Y=length of cloaca (in mm.), and X=width of disc (in cm.). In fishes over this size the cloaca shows greatly accelerated relative growth rate in many individuals and the range of cloacal length measurements increases enormously, reaching and retaining maximum values in fishes of about 67–76 cm. (inclusive) disc widths.

In Figure 7 the length of the cloaca in individual fishes of 5-cm. size-groups, from 36-cm. disc width upwards, is plotted. In this figure the cloacal length measurements produce an approximately symmetrical bi-modal curve in the size-group 66–70 cm. disc widths. From perusal of Figures 6 and 7, therefore, the following conclusions can be drawn concerning the females of *R. clavata* in the English Channel area :—

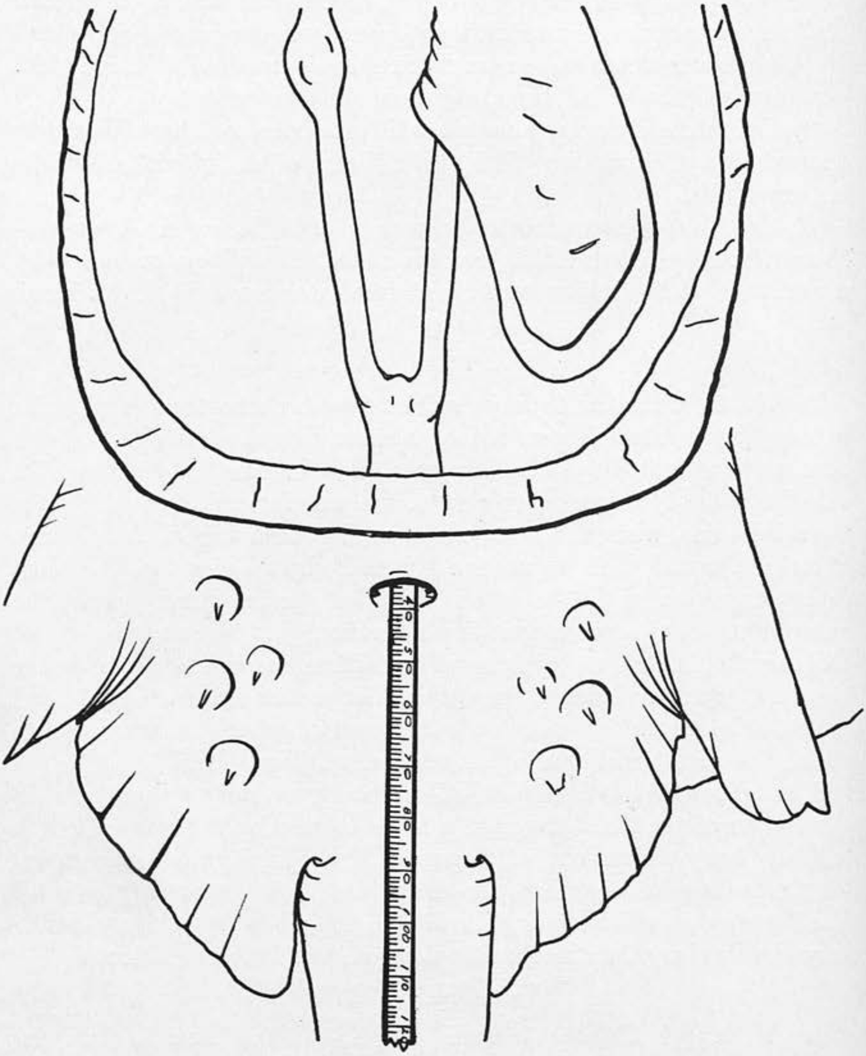

FIG. 4.—*R. clavata*—juvenile female ; 65 cm. disc width ; 36 mm. cloaca length. Dissected to show cloaca. Note immature left ovary (left *in situ*), and small shell gland. $\times \frac{2}{3}$. (For further explanation see text pp. 887 and 893.)

(1) that in any sample of female fishes of this species in which no individual exceeds about 65 cm. in width of disc the great majority will be immature juveniles. This will hold true whether the sample be restricted to any arbitrary size-group of small range or consists of fishes

at all sizes up to the 65 cm. (maximum) disc width. Over most of this range samples of restricted size-groups will consist of 100 per cent

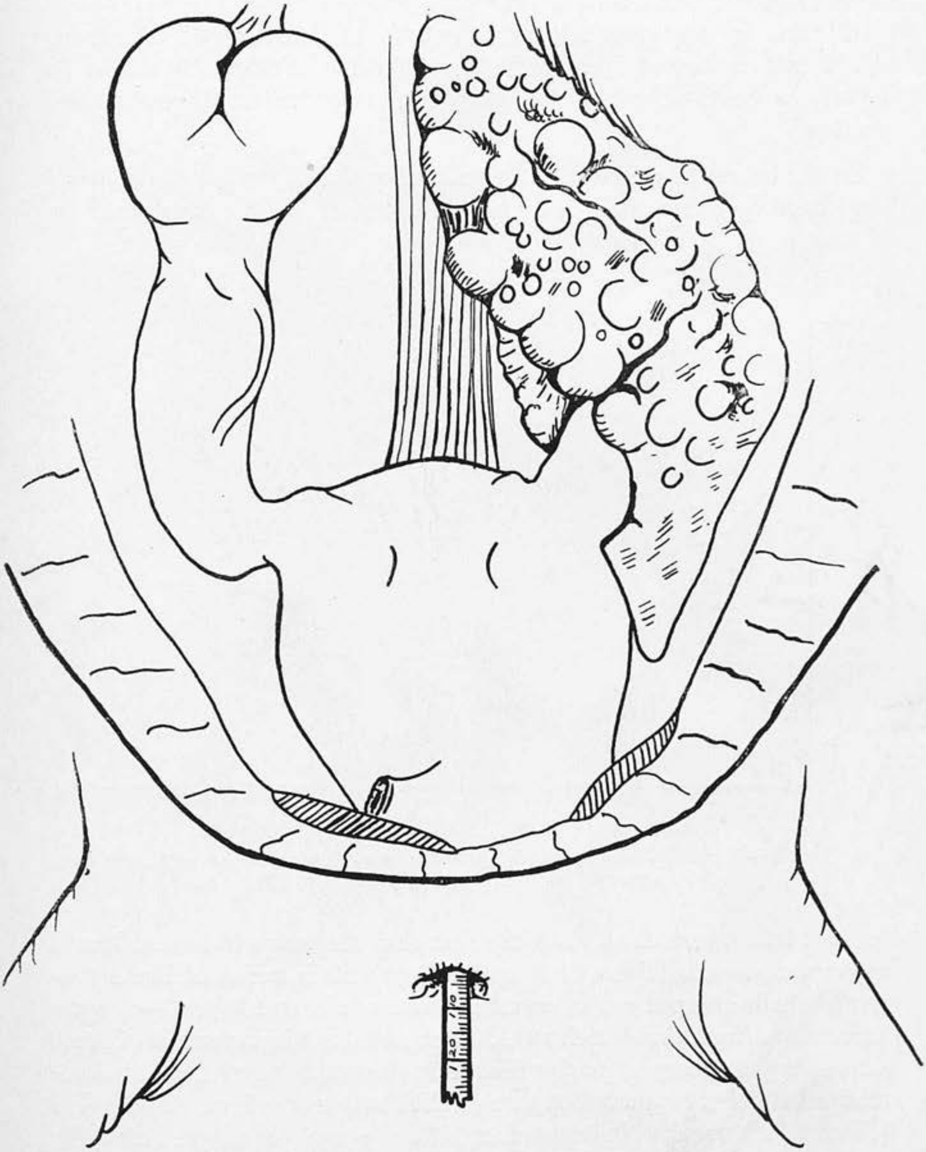

FIG. 5.—*R. clavata*—mature female; 72 cm. disc width; 102 mm. cloaca length. Dissected to show cloaca. Note also developing eggs in ovary and large shell gland. $\times \frac{2}{3}$. (For further explanation see pp. 887 and 893.)

juveniles, but samples at or near its extreme upper limit will contain a certain proportion of individuals at more advanced stages.

(2) that, similarly, in any sample which includes no fishes of less than approximately 70 cm. disc width, the majority—but not all—of the individuals will be mature adults.*

(3) that in any representative sample of females of size-groups 66–70 cm. (inclusive) disc widths, juveniles and adults will tend to be equally represented, while adolescents at all intermediate stages will also be found.

In the course of this work, the possibility that, after all one season's eggs have been deposited, the cloaca may return to its virgin condition

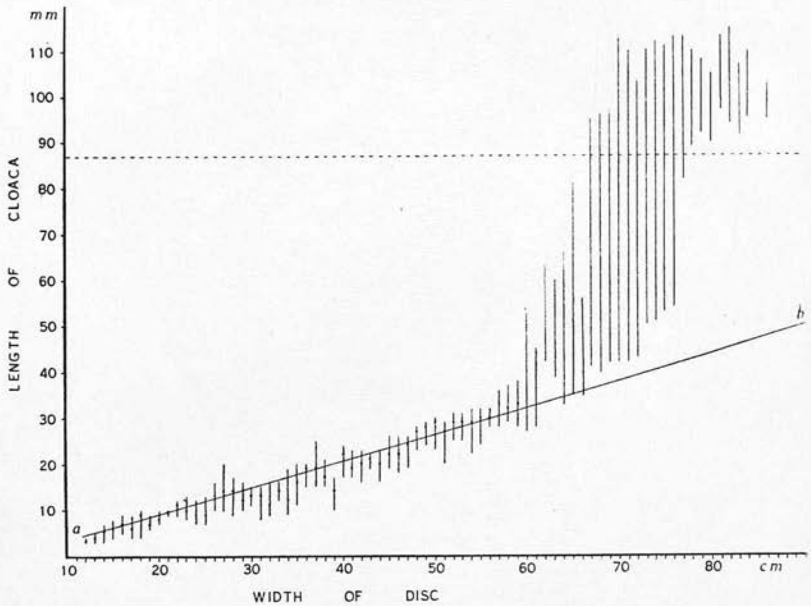

FIG. 6.—*R. clavata*—cloaca length plotted against disc width in centimetre size-groups. (For explanation see text p. 893.)

has not been overlooked. But the fact that the range of cloacal length measurements in all fishes of 76 cm. and upwards in width of disc is relatively small, grouped around a mean value of about 100 mm.—a figure far removed from that which would be expected in virgin females of those sizes—suggests very strongly that this does not happen. This conclusion is further supported by these additional observations. On Newlyn (Cornwall) fishmarket, in September, 1932, the plan was adopted of trying to find a fish of 76 cm. disc width or over with a small cloaca of say 50 mm. length or less. Though many hundreds of fishes were examined, including a large number with fully spent ovaries, the shortest cloaca length

* Shortest cloaca length recorded in a fully mature fish—87 mm. (*vide* dotted line, Figs. 6 and 7).

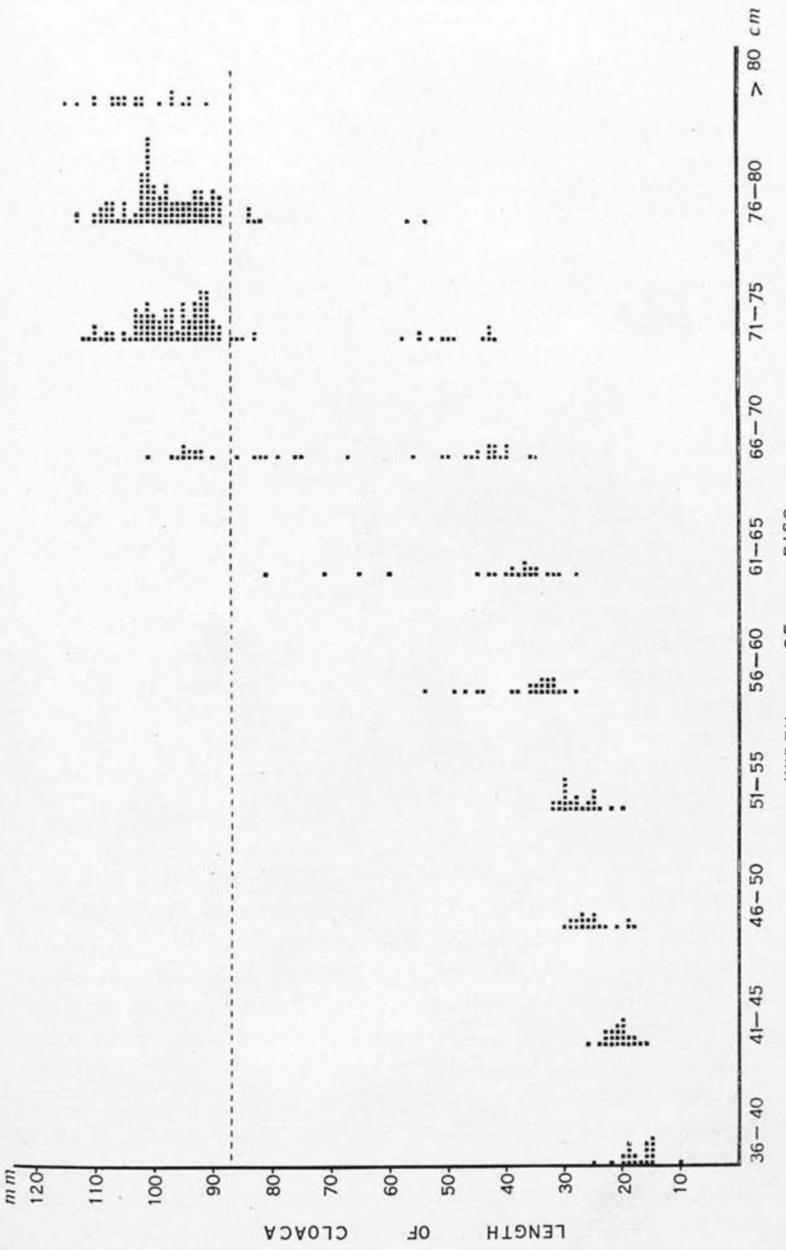

FIG. 7.—*R. clavata*—cloaca length plotted against disc width in 5 cm. size-groups. (For explanation see text p. 893.)

recorded was 87 mm. This was in a gravid female of 76 cm. disc width and containing in each uterus an egg ready for deposition.

IV. Practical Applications.

A. It will be seen from Figure 2 that the 44-cm. (centimetre) size-group of male fishes contains the smallest individuals which show unmistakable acceleration in the relative growth rate of the claspers, thus indicating that they have entered the adolescent phase. The 50-cm. (centimetre) size-group contains the smallest fishes which have become fully mature.

It may with safety be assumed that the first (smallest) fishes to enter the adolescent phase will be also the first (smallest) fishes to reach puberty. It would thus appear that in the males of this species, the adolescent phase occupies roughly the time required to grow round about 6 cm. in width of disc.

Now the results (unpublished data) of the marking experiments so far carried out (*vide* p. 1) indicate that the adolescent males of *R. Clavata* grow at the rate of from about 3 cm. to 5 cm. disc width in the course of one annual growing period. The experiments are being continued and full details will be published in a subsequent paper. But sufficient data have already been collected to suggest that the above figures are reasonably reliable. If this be so, it would appear that in the males of this species the adolescent phase normally occupies rather more than one and not more than two growing periods. From this it may reasonably be concluded that these fishes enter the adolescent phase during one growing period and reach puberty during the growing period of the following year, the time occupied by the changes extending over part or all of the two periods.

In the females (Fig. 6) the difference in size between the smallest fishes to enter the adolescent phase and the smallest to reach puberty appears to be most frequently about 7 cm. disc width. Although females grow rather more rapidly at this stage than males, this difference in size represents in them too the growth increment of more than one and not more than two growing periods. The period of adolescence would appear, therefore, to be the same in both sexes.

B. It has been recorded in a previous paper (**5**, p. 617) that, on certain fishing grounds near Plymouth, there is in the spring months of every year, a congregation of large and fully mature Thornback Rays. At the same time that these adult fishes are being landed by fishing boats using fixed nets, other landings are being made by vessels using long lines or " boulters " on different grounds in the vicinity. A marked feature of the fishes caught on these lines at this time is that they frequently contain a high proportion of adolescent individuals. As with the adults from the nets (**5**, p. 617), so also with these adolescents, a landing will often consist almost entirely of one sex, either male or female. From consideration of the data set forth above it seems likely that these adolescent fishes, typical of " boulter " landings in the spring, entered the adolescent phase during the growing period of the previous year and that the majority, at any rate, of the year-class to which they belong will reach puberty during the growing period immediately following—i.e. later on in the same year. By the ensuing spring these young adults will have joined the shoals of mature fish which will populate the fixed-net fishing grounds at that time.

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5. —— Rays and Skates of Devon and Cornwall. III. The Proportions of the Sexes in Nature and in Commercial Landings, and their Significance to the Fishery. Idem, p. 611.

Migrations and Growth of the Thornback Ray (*Raia clavata* L.)

By

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With 2 Figures in the Text.

I. Introductory.

Although workers in several European countries (England, Germany, Russia, Scotland) are stated (**5**) to be carrying out marking experiments on rays or skates, the writer is not aware of any recently published account of the results of any of these researches. Fulton (**4**, p. 191), however, records that in the years round about 1890 he marked 71 thornback rays (*R. clavata*) and 23 specimens of grey skate (*R. batis*) in Scottish waters. Two of the thornbacks and one skate were subsequently recovered. Of the former, one—about 36·5 cm. in width* on marking—remained at liberty for about three months before being recaptured and had travelled about 13 miles from the place where it had been set free. The other—35 cm. in width—remained at liberty for 278 days and travelled about six miles. The single skate, recaptured after only 10 days, had in that time changed its position by 10 miles. No records of size increments are given.

In order to collect data on the migrations and growth-rate of thornback rays in the English Channel, marking experiments have been carried out on certain inshore fishing grounds in the vicinity of Plymouth. For various reasons, not least of which is the high price† of these fish, the numbers involved are somewhat small—compared with those of plaice-marking experiments in the North Sea, for example. Nevertheless, the results already obtained are of such interest that it seems worth while presenting them at this stage.

After considerable preliminary experimentation with several types, a mark consisting of two vulcanite discs, one white and one black, was selected for use. On the white plate the identification letters and serial number are stamped in black (*vide* **5**, p. 139). The mark is placed on the

* In these fishes, width of disc is the most convenient measure of size.

† Full market value (current price) is paid for a returned fish, in addition to a reward of two shillings if full particulars concerning it are furnished. Rays are prime fish, and as much as seven shillings (inclusive) has had to be paid for the recovery of a marked individual.

right wing (pectoral fin) of the fish, the white (numbered) plate above and the black one below. It is found that in thus having a white disc on the dark, upper surface and a black one on the white, under side, the mark is more readily observed by fishermen when a marked fish comes on board. This is of especial importance with regard to this laboratory's own research vessel in which, when a haul of fish arrives on deck, a marked individual at once catches the eye and is immediately transferred with all speed to circulating sea-water. If, as is usual, it remains vigorous, it is returned alive to the sea after its measurements have been taken. In this way repeated captures of the same fish have been made and valuable data not otherwise obtainable have been acquired (*vide*, pp. 609 and 612 *infra*).

For fishes of about 30 cm. and over in width of disc, mark plates 15 mm. in diameter are used. To all fishes of smaller size mark plates of only 8 mm. diameter are affixed.

II. Migrations.

Although rays are only moderately plentiful in the immediate neighbourhood of Plymouth, where these experiments have been carried out, there is one small fishing ground on which at least a few thornback rays can usually be found at all seasons. On this ground, locally known as the "Corner" (*vide* Fig. 1—shaded area), between 28th November, 1930, and 24th May, 1935, 538 thornbacks have been captured and released again after marking. Releases on other grounds in the vicinity (Fig. 1) have been: Cawsand Bay, 49; Bigbury Bay, 30; Plymouth Sound (inside Breakwater), 7. Of this total of 614 releases, 203 individuals (approximately 33 per cent) have been recaptured after periods varying from 12 to 1357 days. Details of these recaptures are given in Table I.

TABLE I.

Distances Travelled by Recaptured Fish.*

Place released.	Number released.	Number recaptured and distance travelled. Stationary.	Up to 5 miles.	5–20 miles.	20–50 miles.
"Corner" . . .	528	117^{256}	15^{240}	39^{334}	10^{300}
Cawsand Bay . . .	49	2^{71}	3^{705}	5^{391}	1^{415}
Bigbury Bay . . .	30	5^{363}	1^{179}	2^{721}	
Plymouth Sound . .	7		1^{312}	1^{82}	
Totals .	614	124^{280}	20^{311}	47^{350}	11^{311}

From this table it will be seen that of the 202 fishes whose place of recapture is known, no less than 124, or approximately 61 per cent of them,

* Indices refer to average number of days free.

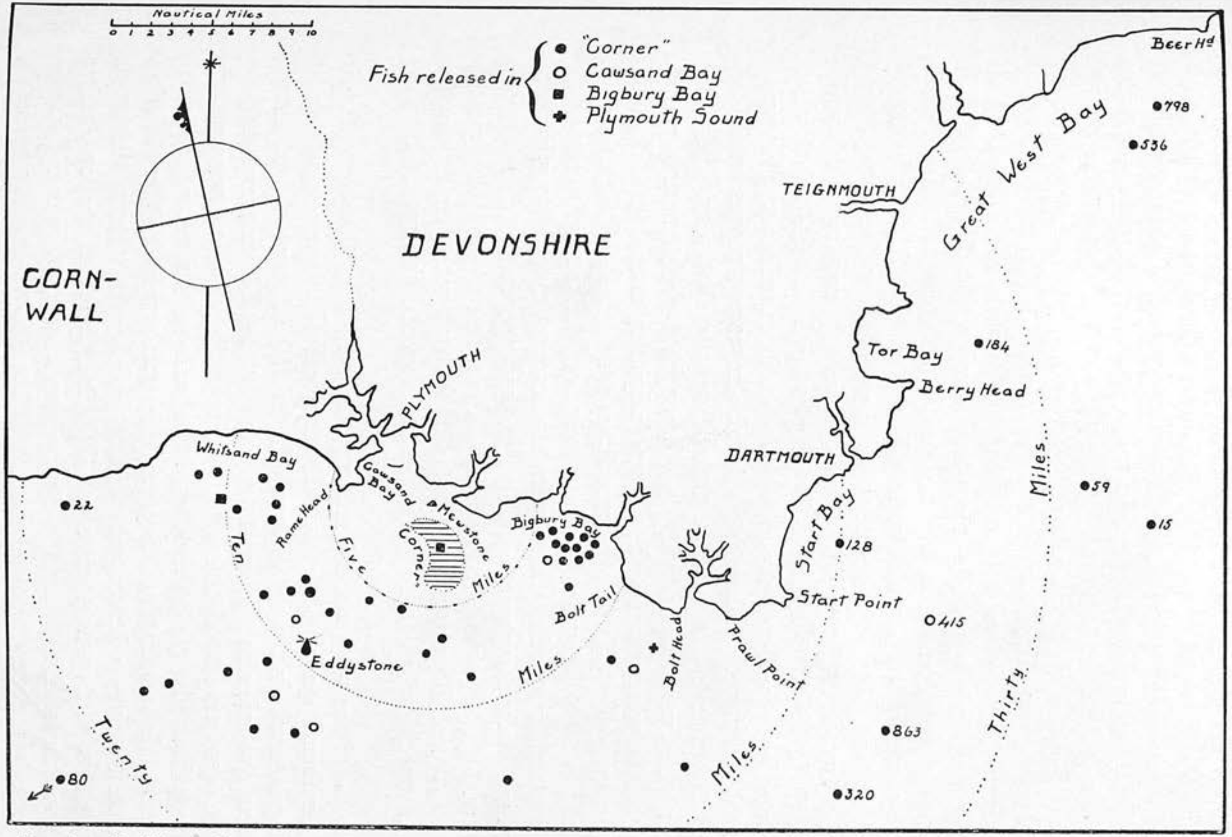

FIG. 1.—Positions of recapture of marked rays which had moved more than 5 miles. Fishes which had exceeded 20 miles have period of liberty shown (in days). For further explanation see text p. 608.

·····–·····– =	circle of 5 mile radius from Mewstone.	·· ·· ·· =	circle of 20 mile radius from Mewstone.
··········· =	,, 10 ,, ,, ,, ,,	··· ··· =	,, 30 ,, ,, ,, ,,

were retaken on the exact spot* where they were set free, and this in spite of the fact that the times which had elasped between marking and recapture again varied from 12 to 1357 days. These returned fish came in at all seasons of the year, and the average period of absence was 280 days. One hundred and forty-four individuals, or 71 per cent of the recaptures, had moved less than 5 miles while only 11 had travelled over 20 miles. Not a single fish has as yet been returned from a distance greater than 50 miles from the point where it was set free.

In Figure 1 are plotted the positions† of recapture of all fishes which had changed their location by more than 5 miles, the different symbols indicating place of release in each instance. The great majority of these recaptures are of fishes which were released on the "Corner" ground (closed circles). Six had been set at liberty in Cawsand Bay (open circles); two in Bigbury Bay (closed squares); and two just inside Plymouth Breakwater (crosses). Bearing in mind that 144 fishes which had moved less than 5 miles are not plotted on it, examination of Figure 1 shows very clearly that there is no definite migratory movement of fish from these grounds. It must be noted, however, that most of the fish marked were immature individuals. Throughout their growing period, therefore, the young thornbacks show no migratory movement. There is simply a very slow diffusion of some fishes outwards in all directions.

Unfortunately, because of their scarcity on the trawling grounds, a sufficient number of adult thornbacks has not been marked to yield data concerning their movements. There is evidence from other sources, however (**1**, p. 20), which suggests that a certain amount of migratory movement (probably not very extensive) is shown by the sexually mature fish. A special effort is now being made to trace the extent of these migrations.

Because of the very marked non-migratory habit of the young fish it has been found possible to capture the same individual more than once at varying intervals in the same place. Of the 150 fishes which had moved less than five miles subsequent to marking, 23 have been recaptured by our own vessel, measured, and returned alive to the sea where, presumably, they are still at liberty. In addition, 10 fishes have been recaptured more than once. In one instance the same fish was caught by the *Salpa* no fewer than 4 times within a year after it had been marked, at intervals varying from 13 days to $4\frac{1}{2}$ months. This fish, therefore, was on a ship's deck five times within 12 months, having been trawled up on each occasion from exactly the same place in about 25 fathoms of water. It was caught

* i.e. as nearly as can be ascertained at sea. As the grounds in question are all close by the land, the positions were fixed with considerable accuracy by the use of landmarks on shore.

† One fish was recaptured beyond the limits of this chart at a point 22 miles farther on, in the direction indicated by the arrow.

again a sixth time, still in the same place, 14 months after marking. Unfortunately, on this final occasion the capture was effected by a commercial vessel which killed it. Details of this and other repeat captures are given in Table II.

TABLE II.

RECORDS OF REPEAT CAPTURES.

Serial No.	Date marked.	Dates recaptured. I	II	III	IV	V	Whether released again.
12	13/2/31	8/4/32	10/5/33				No
30	do.	5/2/32	22/5/32				Yes
51	10/10/31	8/12/31	21/12/32	29/3/33			Yes
63	do.	9/2/32	6/8/35				No
68	do.	24/8/32	26/9/33				No
133	23/12/31	22/1/32	14/5/32	13/9/32			Yes
226	25/4/32	22/5/32	25/8/32	5/1/33	18/1/33	1/7/33	No
285	12/5/32	29/7/32	7/12/32				No
103 S	25/4/32	22/3/33	26/1/34	23/4/34			Yes
143 S	12/5/32	15/7/32	2/8/32				No

All the fishes recorded in the above table were captured and released on the " Corner " grounds in from 20 fathoms to 25 fathoms of water, and all except one were in every instance recaptured exactly where they had been originally set free. The single exception was No. 63 which, in the interval between its second and third (final) captures, had moved to Bigbury Bay. Where in this table fishes are recorded as being no longer at liberty it means that, on the final occasion of their capture, they were taken by a commercial vessel and returned dead to this laboratory. Those still at liberty were on every occasion taken by the laboratory's research vessel and returned alive to the sea after measuring.

It is important further to note that all of the fishes included in Table II —except No. 63—were immature at the time of marking and were still immature at the time of their final recapture, the largest, a female (No. 285), being then approximately 49·5 cm. in disc width. The single individual (No. 63) which on its final capture was found to have moved a few miles away was an adolescent female 64·5 cm. in width.

In trawling for rays for marking purposes each haul has seldom been less than 1 hour and never exceeded 2 hours in duration. That numerous fish have survived repeated capture, as recorded in Table II, indicates that they can successfully withstand pretty severe treatment. But still further, and at first rather unexpected, evidence of their capacity to withstand rough handling has been obtained. During marking operations, immediately after a catch of fish has been brought on board, the trawl frequently has been lowered again at once and the captured fish marked and released while fishing continued in progress. This is now the routine method of working. In these circumstances it occasionally happens that a newly marked fish goes straight to the bottom and is caught again forthwith in the advancing trawl.* Most fishes taken twice in rapid succession in this way have survived the double capture and several have been caught again after further periods of liberty. One individual (222 S), a young male 22·5 cm. in width, was caught and brought on board three times on the day of marking and, having survived, was finally released only to be taken yet again after an interval of approximately 11 months. Details of this and other repeat captures on the day of marking, and the further history of each fish, are given in Table III.

TABLE III.

Repeat Captures on Day of Marking.

Serial No.	Details of capture on day of marking.	Subsequent history.
222 S.	Retaken twice, after marking, in consecutive hauls of the trawl.	Caught again after 333 days' liberty. Still free.
242 S.	Retaken once after first release on day of marking.	Caught again after 169 days' liberty.
12	Do.	Caught again after 14 months' and 25 months' liberty (*vide* Table II).
209	Do.	Caught again after 111 days' liberty
266	Do.	,, ,, ,, 27 ,, ,,
397	Do.	,, ,, ,, 12 ,, ,,

In addition, eleven other individuals have been retaken once after first release on the day of marking but have not been heard of again.

Three small thornbacks, however, each under 14 cm. in width, which at different times were taken in consecutive hauls, failed to recover after the second capture. Only on one occasion has a larger fish (48 cm. wide) failed to recover after two captures. This fish, when it arrived on deck the second time, received a severe knock from a large stone which had found its way into the cod end, the injury so received being the probable cause of death.

It is hoped to carry out further tests on the survival powers of rays of different species. The results so far obtained, however, suggest that where these fishes form an important part of the catch—as in English Channel

* Rays returned to the sea after having been in the trawl, irrespective of whether or not they have been marked, usually swim about at the surface for a considerable time before descending to the bottom.

waters—it would well repay commercial trawl-fishing vessels to take the shortest possible hauls which are consistent with fishing efficiency, and to return at once to the sea all rays which are too small to be marketable. Possibly the very smallest individuals might not recover, but the larger unmarketable sizes would almost certainly live. Being non-migratory, these young fish would remain on the same grounds until they reached saleable size; they would not move away to another area where other fishermen (perhaps less careful of their own stocks) would reap the benefit. The non-migratory habit of these fishes in their growing stages, coupled with a relatively long juvenile life (*vide* p. 614 *infra*) is also important in that it increases the possiblity of reducing the stock on any particular fishing ground by too intensive fishing. Unlike migratory species which are exposed to capture only for so long as they remain in a fishable area, and whose numbers tend to be sustained or replenished by immigrants from other localities, the rays present on fishable ground remain constantly exposed to capture, and their numbers will be augmented only very slowly by gradual infiltration of individuals from adjacent regions where fishing is impossible or less intense.

III. Growth.

Of the 202 recaptured fish whose place of recapture is known, figures relating to size* have been received for 197 of them. Ten of these have been captured more than once and more than one record of growth has been obtained.

In Table IV the mean growth increments grouped at monthly intervals for fishes of 10-cm. size groups are given, the indices denoting the numbers of fish upon which the entries are based. Only 2 fishes of the very smallest size group (10–19·5 cm.) have been returned. It would seem that many of these very small individuals do not survive the ordeal of marking although returned to the sea in very vigorous condition. Notwithstanding that the smaller of the two marks in use is invariably affixed to them, it is relatively an enormous encumbrance to such tiny fishes, not to mention the relative severity of the operation when placing it in position. The use of a still smaller mark is impracticable.

At the other end of the scale, only very few fishes over 60 cm. disc width have been marked, and only one returned. As mentioned above, most of the fishes present on the Plymouth grounds are immature individuals and it is therefore mainly to those sizes, from about 20 cm. to 50 cm. disc width, that the data so far collected apply.

Examination of Table IV shows that, over this range—although there is considerable variation in the data owing to individual differences in

* All measurements are made to the nearest half-centimetre next below.

growth rate—both sexes grow at a rate of from slightly under 4 cm. to slightly over 8 cm. in width of disc in the course of a full year.

In Figure II the growth increments of fishes which several times have

TABLE IV.

Mean Size Increments of Marked *Raia clavata*.

Grouped at monthly (=4-weekly) intervals. Size increments in cm. Indices denote numbers of fish upon which entries are based when more than one.

Months at liberty.	Size group (cm.). 10–19·5 ♂	10–19·5 ♀	20–29·5 ♂	20–29·5 ♀	30–39·5 ♂	30–39·5 ♀	40–49·5 ♂	40–49·5 ♀	50–59·5 ♂	50–59·5 ♀	60–69·5 ♂	60–69·5 ♀	
0			$0{\cdot}17^6$	$0{\cdot}0^4$	$0{\cdot}3^2$	$0{\cdot}0^4$	$0{\cdot}0^2$	$0{\cdot}2^3$	$0{\cdot}5^2$	0·0			
1				$0{\cdot}1^4$	$0{\cdot}5^5$				$1{\cdot}3^2$	0·0			
2			0·5	0·5	$2{\cdot}3^2$	$1{\cdot}2^3$	0·5			$0{\cdot}3^2$		0·5	
3			$1{\cdot}2^3$		$2{\cdot}0^3$	$1{\cdot}2^3$	$0{\cdot}5^2$		0·0	2·0			
4			$2{\cdot}0^2$		$1{\cdot}5^2$	$1{\cdot}8^3$	1·0	$0{\cdot}5^3$		1·0			
5					0·5	1·0	3·0			$2{\cdot}0^2$			
6			0·0	3·0	$3{\cdot}1^3$	3·0		0·5	2·0	$3{\cdot}0^2$			
7				1·5	$2{\cdot}5^2$	$4{\cdot}2^3$	$3{\cdot}8^2$	3·5					1 year.
8			$3{\cdot}3^2$		3·5		2·5	$3{\cdot}0^2$					
9			6·0	4·5	5·0	$3{\cdot}3^3$		$5{\cdot}2^3$	0·5				
10			5·0			4·5		5·5	3·5	6·5			
11			2·5		3·5	$3{\cdot}0^2$	3·0	6·5	5·0				
12				4·5	8·0	3·0							
13			5·5				$5{\cdot}5^2$						
14			$7{\cdot}3^2$			$4{\cdot}5^2$		6·5		9			
15		5·5			7·5	$7{\cdot}3^2$	5·5		5·5				
16					9·0	11·5				$3{\cdot}8^2$			
17			$8{\cdot}3^2$		5·5	$7{\cdot}0^2$							
18			8·0					8·0					
19					$9{\cdot}8^3$	16·0	7·5	9·5					
20					7·5					11·5			2 years.
21						4·5	$10{\cdot}5^2$	6·0					
22							5·5						
23					4·5								
24							5·5						
25			17·0		12·0								
26				16·0									
27										18·0			
28								13·0					
30						17·5							
31							$7{\cdot}8^2$						
33	7·5												3 years.
34						6·5	12·5			11·5			
36						16·5	12·0						
39				13·0									
43						31·0							
45			23·0				9·0						
48				$29{\cdot}5^2$									4 years.
52													

been captured are shown graphically.* From this figure it will be seen that fishes No. 30, 51, 133, 226, and 103 S, which happened to be caught

* It should be noted that the lines joining the points plotted in this graph are inserted simply to facilitate reference to the several records for each fish; they have no mathematical significance.

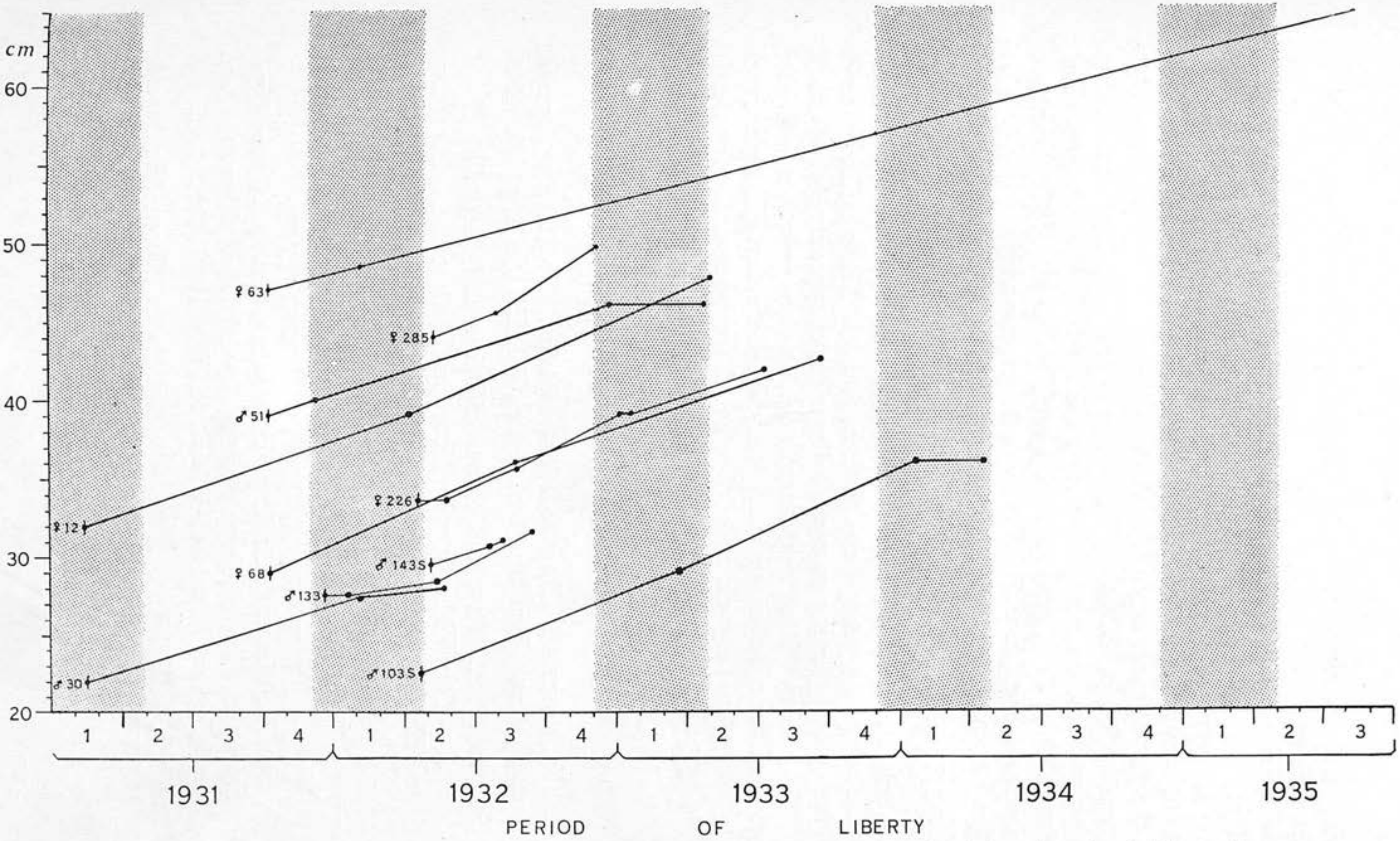

FIG. 2.—Growth of fishes for which more than one record has been obtained. The sex and serial number of each fish are given. Stippled areas = winter (non-growing) periods. ⏀ indicates first measurement and time of marking.

twice in the course of a winter period, show little or no growth in the winter interval. This winter period of slackened growth rate appears to extend from about the beginning of December until the end of April.

From this figure, too, it will be seen that the rate of growth in both sexes is approximately the same over the size range represented. For reasons already stated no data are available from marking experiments on the growth rates of the largest size groups. Observations on market categories (**3**, pp. 890 *et seq.*), however, reveal that in the males first-maturity is reached at or shortly after a disc width of 50 cm. is attained, and that thereafter their growth rate rapidly falls off. Male thornbacks seldom exceed and usually fail to reach 60 cm. disc width.

The females, on the other hand, do not reach first-maturity until they have attained a disc width of from 65 to 70 cm., and old adults of over 80 cm. disc width are not uncommon. Since both sexes grow at about the same rate until the male reaches first-maturity it follows that the males become adult at a younger age than the females. Thornback rays hatch out from the egg having an average disc width of approximately 8 cm. (**1**, p. 595). Taking 6·0 cm. per annum as an average growth rate in both sexes until the onset of sexual maturity, it follows that the males reach this stage when they are about 7 years of age whereas the females do not become sexually mature for another 2 years or so.

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B.

MACKEREL

(Scomber scombrus L)

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CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL, *SCOMBER SCOMBRUS* L.: MACKEREL MIGRATIONS IN THE ENGLISH CHANNEL AND CELTIC SEA

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Zoologist at the Plymouth Laboratory

(Text-figs. 1–6)

Introduction

The common mackerel (*Scomber scombrus* L.) is one of the important European food fishes. Forty-two species of commercial sea fishes are listed by the Conseil Permanent International pour l'Exploration de la Mer in its *Bulletin Statistique des Pêches Maritimes* as being landed in northern and western Europe. Four-fifths of these landings are made up of only twelve important food fishes, of which the mackerel is one. In 1937 (Thompson, 1939), the last year for which full normal figures are available,[1] approximately $1\frac{1}{4}$ million cwt. of mackerel were landed by all the countries of northern and western Europe (excluding Russia), having a total value, as nearly as can be ascertained, of just over £887,000. To this total Great Britain, Eire, and Northern Ireland contributed rather more than 14 % of the quantity and almost 13 % of the value. During the inter-war period, however, Britain's contribution had fallen steadily, her share in 1913 (a year that has long been used as a standard of comparison) being no less than 49 % of the total quantity and 31 % of the total value of all mackerel landings.

Of the British Islands, England is the chief mackerel-fishing country. Just prior to the outbreak of the recent war her total landings were some 140,000 cwt. valued at about £80,000. It is a noteworthy fact that rather more than one-third of this quantity was landed at the single small port of Newlyn, in Cornwall (Figs. 1 and 2). It is still more surprising to note (Fig. 1) that during the four years 1923–1926 more mackerel were landed at Newlyn than at all other ports in England and Wales put together.

There are, in normal times, two distinct mackerel fisheries worked from Newlyn. One is a long-distance, deep-sea fishery carried out by steam drifters (of the normal herring drifter type) in the Celtic Sea far to the westward of the Scilly Islands—except towards the end of the season when fishing takes place nearer land. This fishery will be called the *Newlyn Deep-Sea Fishery* for

[1] The figures for 1938, though published in 1944, are not complete.

mackerel. The other is an inshore fishery that takes place in inshore waters off the northern coasts of the Cornwall and Devon peninsula. In it, boats from other small ports take some part, but Newlyn is the chief centre. This fishery will therefore be called the *Newlyn Inshore Fishery* for mackerel.

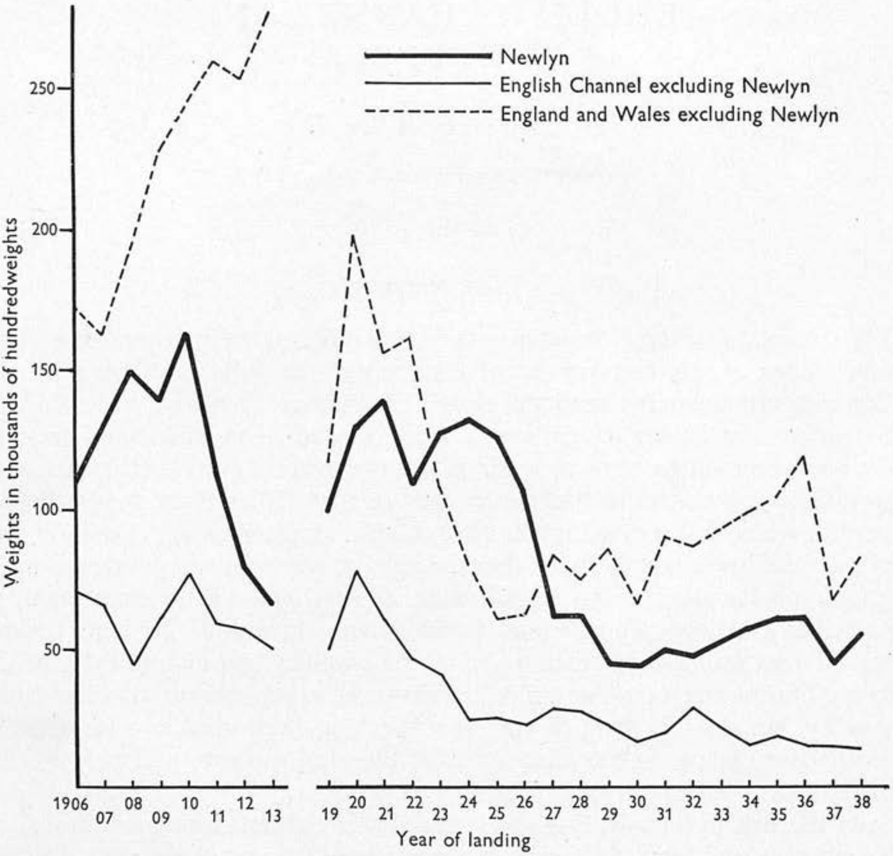

Fig. 1. Mackerel landings in thousands of hundredweights at Newlyn (——); in England and Wales excluding Newlyn (----); and at English Channel ports excluding Newlyn (——). From *Sea Fisheries Statistical Tables* for the years 1906–1938 inclusive.

At Newlyn, then, in normal times, by far the most important mackerel fishery in Great Britain takes place, and it was at this port that most of the data for this investigation were collected.

The Newlyn mackerel fisheries were temporarily suspended during the 1914–18 war and again in the Second World War. Unfortunately, normal fishing has not yet been resumed after this second interruption owing to the uneconomic prices obtainable for mackerel in comparison with operating costs.

In past years there was also a flourishing mackerel fishery farther up the English Channel at Plymouth; but the Plymouth fishery, for purely economic reasons, gradually declined and came entirely to an end about the year 1926. This fishery will be called the *Plymouth Channel Fishery* for mackerel. A brief but detailed description of all these fisheries will now be given because an adequate knowledge of them is necessary for obtaining a clear picture of the migratory movements of the mackerel upon which they all depend.

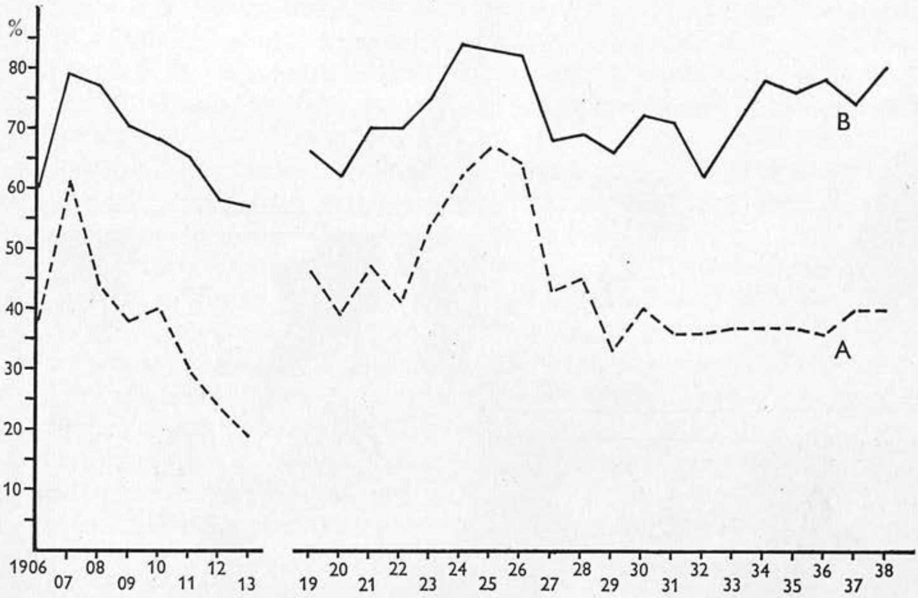

Fig. 2. Percentage contribution by Newlyn to total landings (*A*) in England and Wales; (*B*) at English Channel ports, from 1906 to 1938 inclusive.

The Plymouth Channel Fishery

Although this fishery no longer exists, it is necessary to examine its previous activities in considerable detail, for mackerel are still present on the grounds worked by it long ago and the same migrations still take place by fish that are now untouched by any catching instrument.

The mackerel season began off Plymouth towards the end of December or early in January and boats from east and west used to converge on the port in large numbers to take part in it. Ridge (1889, p. 72), reporting on the fishery of 1888, states that fishing began in that year in January and that vessels from Yarmouth, Lowestoft, Newhaven, Brighton, Eastbourne, Hastings, Porthleven, Newlyn, and Mousehole arrived to take part in it. According to Calderwood, (1892, p. 279) the Plymouth drift-net fleet alone at this season used to number between three and four hundred sail.

In a series of reports on fishing in the neighbourhood of Plymouth, in different months of each year towards the close of last century (1892 and 1893),

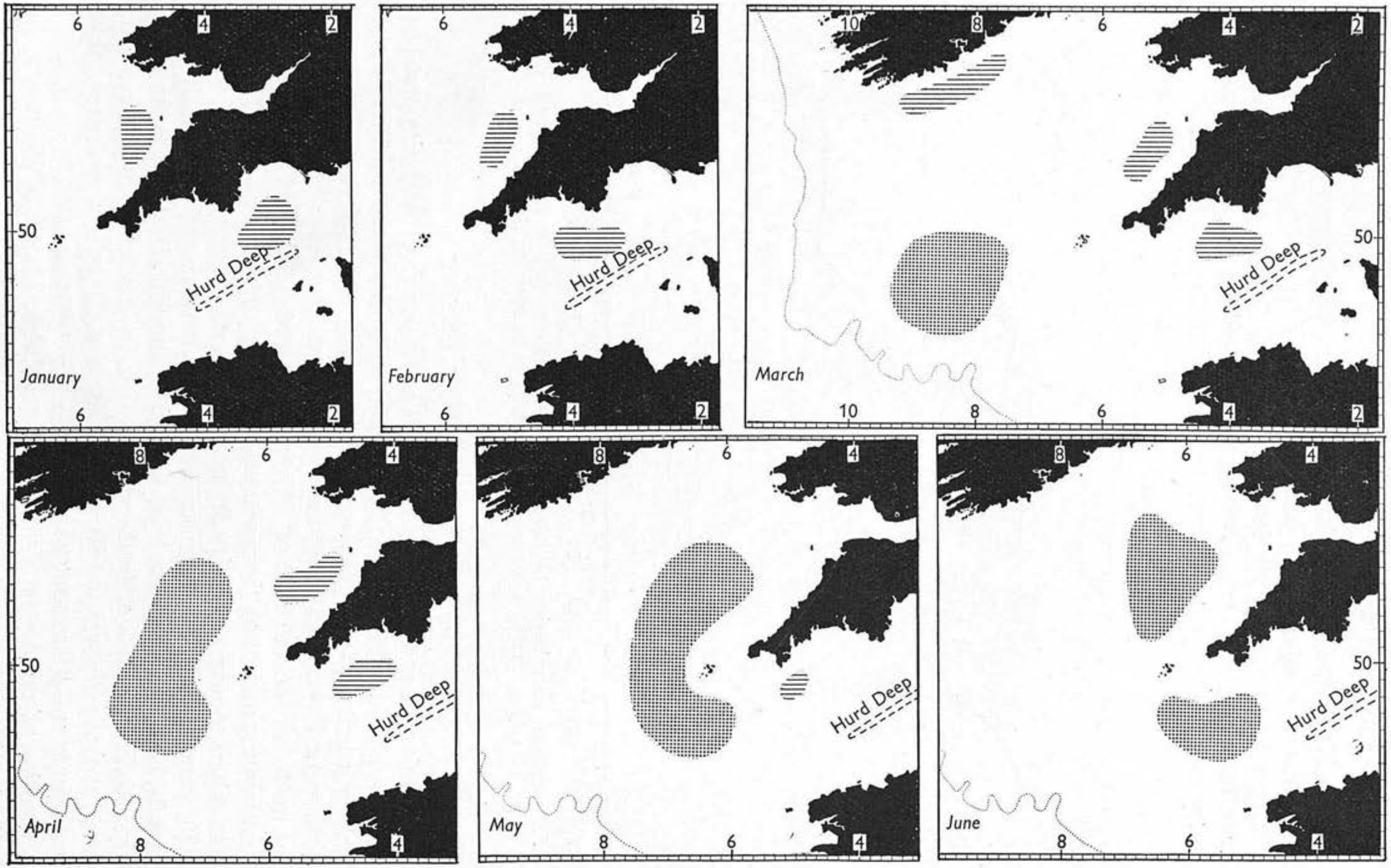

Fig. 3. Generalized charts showing times of fishing for mackerel in different parts of the English Channel and Celtic Sea. *Hatched* areas, inshore fisheries; *stippled* areas, deep-sea fishery (*vide* pp. 519–24). The 100-fathom contour is indicated by a dotted line.

Calderwood constructed a series of monthly charts showing as nearly as possible the kinds of fish caught during each month and the positions of the grounds being worked. From these reports, and from conversations with some of the old fishermen who were active at that time, one finds that in January fishing for mackerel took place on grounds to the eastward of Plymouth, generally from 10 to 30 miles south to south-west of Start Point. As the season advanced the fish had to be sought progressively farther and farther to the westward. By the middle or end of March the fleet would be working from 10 to 30 miles southward from the Eddystone lighthouse (i.e. 20–40 miles to the seaward of Plymouth). By May the best catches were generally to be had on grounds still farther west, and the Plymouth fleet sometimes went as far as 40 miles south-west of Lizard Head before terminating the season's fishery. The time at which this occurred varied from year to year, but was seldom if ever later than the middle or end of May. When this happened many of the east coast boats returned to their home ports to fish no more for mackerel until another 'west-country season' came round. But some of them, together with the west-country boats, proceeded to Newlyn and other Cornish ports to carry on fishing from there on the deep-sea grounds to the westward of the Scilly Islands (*vide* p. 522). This sequence of events in the Plymouth fishery is summarized in Fig. 3 in which the hatched area in the English Channel indicates the extent of the fishing ground and the gradual shift of the fishery from its eastern end in January to its western extremity in May.

It should be noted that these west-going shoaling fish never approach really close to the land, but always remain at some distance from it. This is in marked contrast to what happens when mackerel reappear in the Channel in June after the shoals have broken up (*vide* p. 524). The fish then appear hard by the beaches and in creeks and harbours all along the shoreline in the very shallowest water.

The Newlyn Inshore Fishery

This fishery is confined to inshore grounds along the north Cornwall and north Devon coast. On these grounds, extending roughly from 20 to 50 miles north-north-east of the Longships Lighthouse (Land's End), fishing in normal times begins in December or early January and continues for 3 or 4 months. At the beginning of its season the best catches are to be expected well to the northward and then progressively farther southward as the season advances. The hatched area to the north of the Cornwall-Devon peninsula in Fig. 3 indicates the extent of this fishing ground and the gradual shift of the fishery from its northern end in January to its south-western extremity by about April.

The sequence of events in this area should be carefully compared with that on the fishing grounds in the English Channel (also shown on this chart and already described) and their similarity noted.

The Newlyn Deep-Sea Fishery

The modern great spring mackerel fishery from Newlyn opens in March (Fig. 3) on grounds right out in the open Atlantic far to the westward of the Scilly Islands. It is a drift fishery carried on by steam drifters of the familiar herring-drifter type which come to this port from the east coast ports of Yarmouth and Lowestoft.

Although fishing begins in the first days of the month, it is usually somewhere about the middle of March before the fleet falls in with the main shoals. While the search for them is going on, some of the boats try their luck hard by the Irish coast to the south-west and south of Ireland. From 10 to 20 miles south to south-west of Fastnet Rock and about the same distance off Galley Head and the Old Head of Kinsale are the most favoured localities; and good catches are sometimes made there, but for only a very short time at the beginning of the season (Figs. 3 and 4 A).

The charts in Fig. 4 have been prepared to show the locus of this fishery as indicated by the activities of ten drifters out of a total fleet of twenty-four in 1938—a typical year. The information upon which the charts are based was derived from log-book records kept by each vessel. Every shot made by each of the ten drifters throughout the season is indicated by a dot in the position in which it was made. The fishing of these ten vessels is fully representative of that of the total fleet and gives a true picture of the changes in the locus of the fishery as the season advanced.

It will be seen (Fig. 4 A) that during the first fortnight of March—the opening fortnight—there was only limited fishing, concentrated chiefly near the south coast of Eire. A few exploratory tries were also made over a widely scattered area to the westward of the Scilly Islands. This 'scatter' indicates the absence of good fishing in that locality as yet. By the second half of March (Fig. 4 B) fishing is in full swing with the area of chief fishing intensity located from 70 to 100 miles west to west-south-west of the Bishop Rock, Isles of Scilly. During the first half of April (Fig. 4 C) the best fishing still persists in approximately the same place but slightly less distant. A few tries were also made on northern grounds about 70 miles north-north-west of the Longships (Land's End), but failed to find many fish. By the second half of April (Fig. 4 D) the locus of chief fishing intensity had moved to these northern grounds, all the vessels having for the time being forsaken the 'southern' grounds. During the first half of May (Fig. 4 E) good catches were being taken to the westward of Scilly, but considerably closer to land (i.e. farther to the eastward) and on a slightly more southerly bearing. After the middle of the month (Fig. 4 F) most fish were encountered still farther in towards the mouth of the English Channel, and, being productive of good catches, attracted most of the fleet to this locality. During the first half of June (Fig. 4 G) fish were being caught both to the northward of Scilly and southward from Mounts Bay, the northern

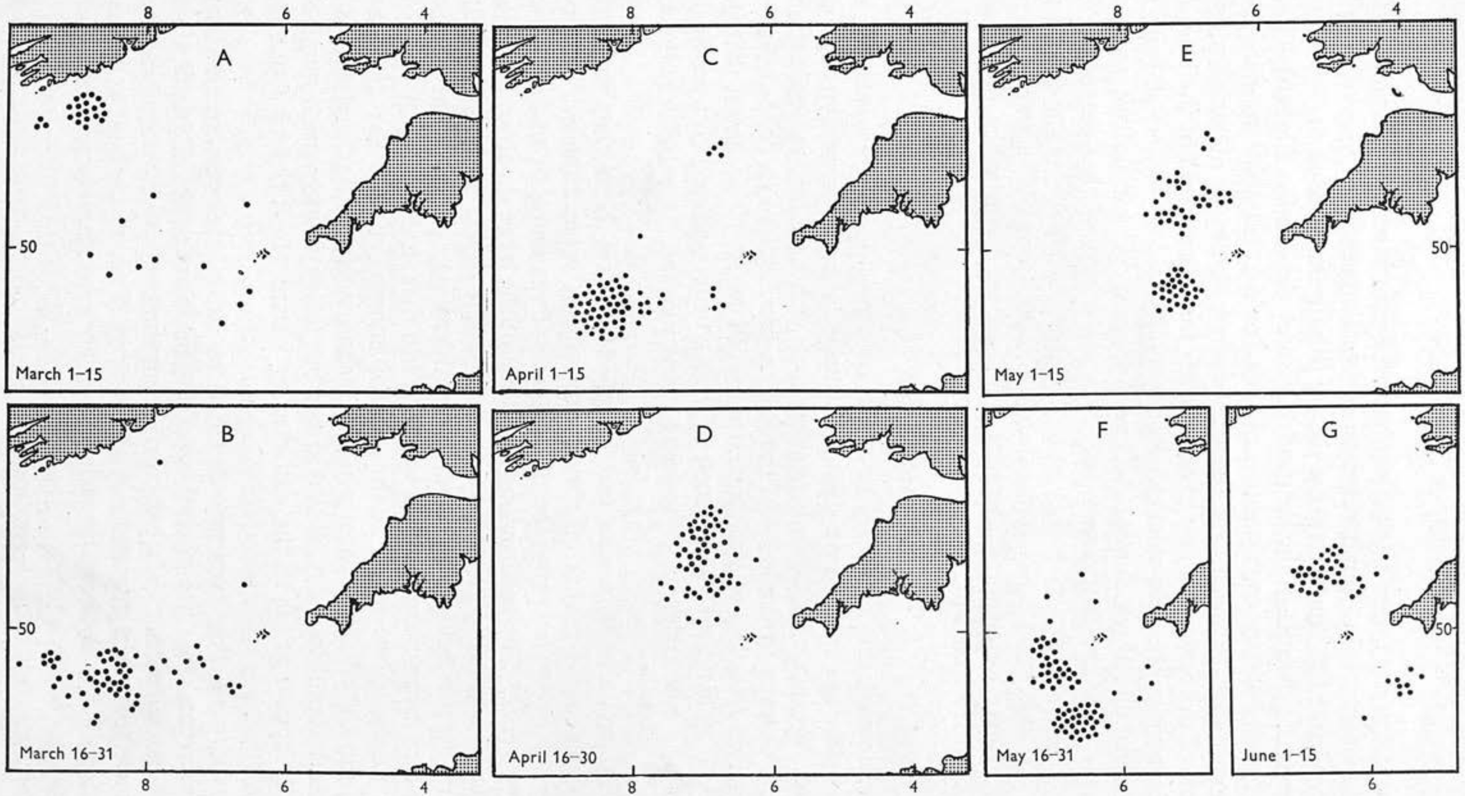

Fig. 4. Locus of mackerel fishing in 1938 by Newlyn-based steam drifters; A, in the first half of March; B, in the second half of March; C, in the first half of April; D, in the second half of April; E, in the first half of May; F, in the second half of May; G, in the first half of June. Each dot represents a 'shot' by one of ten selected drifters.

locality yielding the better catches on the average and therefore attracting the greater part of the fleet. But all catches were now dwindling; on 15 June the last drifter landed its final catch and all the fishing stopped.

Although the changes in the locus of the fishery depicted in Fig. 4 A–G are typical of what happens each year, no two seasons are ever quite the same. In some years, towards the end of the season, best fishing is obtained to the northward of the Scilly Islands; in other years the western end of the English Channel provides the best catches. By about the middle or end of June in every season drift fishing comes to an end, the shoals having so dispersed that this method becomes unremunerative. It is at this time that the mackerel appear in large numbers in shallow waters all along the shores of southern and western England, where they remain until late September, October, or even November, after which they disappear until the next year when the whole cycle of events recurs.

Migrations

It is well known that different shoals of fish appearing in orderly succession in space and time can and do give rise to false appearances of migrations that do not in fact take place.[1] Such phenomena may well underlie, to some slight extent, the changes in the locus of the fishing grounds shown by each of the three fisheries described above. Nevertheless, there can be no doubt that the sequence of events displayed by each of them during its respective season is, in the main, a true reflexion of real and extensive migrations by large bodies of fish.

The almost universally accepted belief has always been that mackerel everywhere, after wintering off-shore, generally in some unknown locality, approach the coasts in spring for the purpose of spawning in shallow water close by the land.[2] The anadromous migration of the large shoals of fish upon which the Newlyn deep-sea fishery depends might appear at first sight fully to conform to this belief; the catadromous migrations of those that support the two other fisheries certainly do not. The fish that are found in the English Channel migrating westward in the opening months of the year disappear offshore, and they do not spawn while in inshore waters. Mackerel eggs are never found in the English Channel in any but insignificantly small numbers and hardly appear at all to the eastward of Lizard Head before about the middle of June.

Close study of the mackerel fisheries in the south-west of England reveals, therefore, that the migrations of the mackerel in the Celtic Sea and English Channel cannot be satisfactorily explained simply by postulating an anadromous spawning migration in the spring of each year and a reverse migration in the late autumn and early winter when mackerel largely disappear

[1] E.g., the herring in the North Sea.

[2] This is fully discussed on pp. 532–4.

from inshore surface waters. Still less will this explanation suffice in the light of the knowledge we now possess that in all this wide region there is only one important spawning ground lying far out to the westward of the English coast. This spawning ground has been surveyed in detail and the results described elsewhere by Steven & Corbin (1939) and more fully by Corbin (1947). From the information contained in those papers a generalized diagram has been

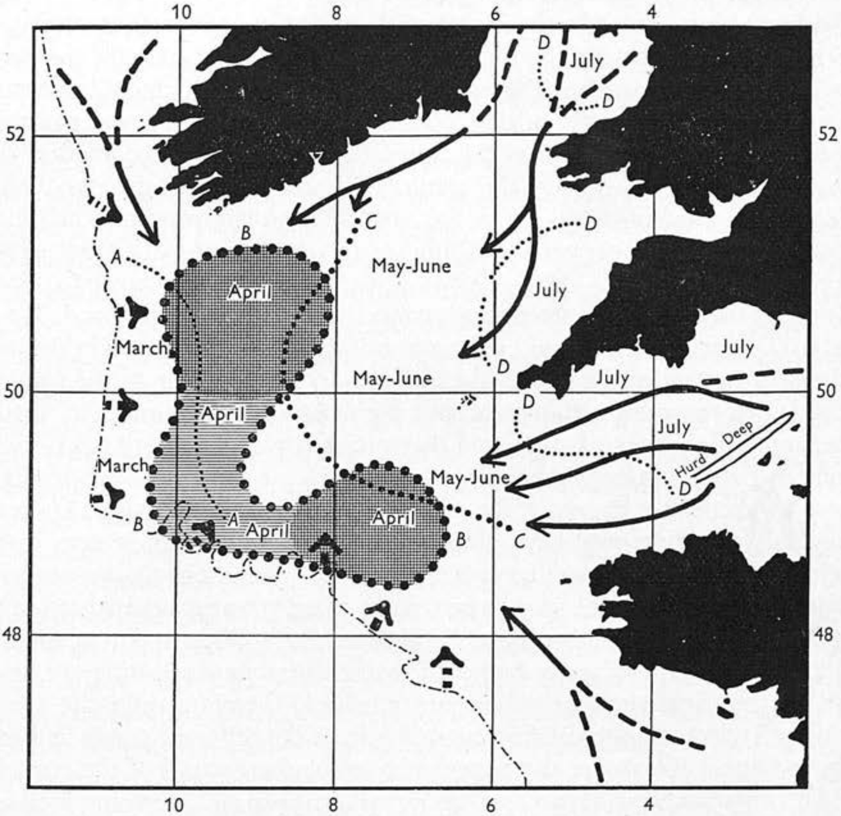

Fig. 5. Generalized diagram indicating the migrations of the mackerel in the English Channel and Celtic Sea in relation to the spawning ground. For further explanation see text, pp. 525–6. ·–·–·–·– = 100-fathom contour.

prepared (Fig. 5), from which can be seen at a glance the location of this spawning ground and its relation in space to the mackerel movements revealed by the three commercial fisheries described above.

Spawning on a small scale begins as early as March to the westward of the dotted line *A* in Fig. 5—i.e. in the vicinity of the 100-fathom contour which, in that area, closely follows the outer edge of the great continental plateau lying to the south of Ireland. The greatest intensity of spawning takes place in April in the area enclosed by the dotted line *B*. Within this area there are two sub-areas (darkly stippled in Fig. 5) of maximum egg density—one situated from 40 to 100 miles south of Fastnet, and the other from 50 to 80 miles south-west of the Scilly Islands. It will be seen that these two sub-areas are situated opposite and to seaward of the entrances to the Irish Sea and the English Channel. It may well be that they represent two distinct spawning grounds that meet and overlap, and whose boundaries cannot be distinguished where the overlapping takes place.

Spawning continues after April, but with gradually decreasing intensity, for another 3 months or so, the locus of spawning activity moving the while slowly eastwards towards the English coast. In May and June all spawning has ceased to the westward of dotted line *C*. By July such meagre spawning as still continues is residual and unimportant and is confined to the close vicinity of the land—within the confines of the English Channel, Bristol Channel and Cardigan Bay—i.e. to the eastward and landward of dotted lines *D* in Fig. 5. A few eggs are also found at this time in the Irish Sea (Scott, 1913, 1914*a*, *b*).

In so far as the south-western area is concerned, therefore, it is now definitely established that mackerel begin to spawn at least as early as March in the deep and distant waters of the Celtic Sea near the 100-fathom line to the south of Ireland; that spawning activity reaches a highly intensive maximum in April in waters only slightly less distant; and that such spawning as continues into late spring and early summer in shallow inshore waters is residual and unimportant. Those mackerel that approach the south-western shores of England from the westward in early spring have already got rid of most of their eggs before reaching inshore localities. Those that are already present in coastal waters in the opening months of the year do not spawn there but migrate offshore to the common spawning ground of the region before doing so. The apparent anomaly hitherto presented by various bodies of mackerel migrating in different directions at the same time, now becomes resolved, therefore, into the simple picture of various groups of fish migrating from the different places in which they had spent the winter to the common spawning ground of the region.

The various schools of mackerel do not all arrive in the spawning region at the same time. This gives rise to the decided 'spread' of spawning activity in both space and time. Another contributory factor is that in this species the eggs mature in successive batches that are spawned one after another during an extended spawning period. Ripe translucent ova appear in the ovary distributed widely and irregularly amongst the still unripe yellowish ova, producing a peculiar, speckled appearance that for lack of a better term has been called the 'plum pudding' stage. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, may show no trace of ripe eggs. Unless opened up such an ovary can be, and often has been, described as 'unripe'. In the mackerel, in fact, a fully ripe ovary is never present; the most that is ever found is an ovary containing some ripe eggs. Cunningham (1889,

p. 25) was therefore in error in thinking that the ovaries and testes of all adult mackerel ripen rapidly and simultaneously and that 'all the reproductive products in a given fish are matured and shed within a short space of time'.

The important question now arises, where do the mackerel come from to this Celtic Sea spawning ground? It seems clear that many, perhaps even the majority, must have been in offshore waters prior to March, since we now know that some of them are already spawning at that time in the vicinity of the 100-fathom line (Fig. 5). Although definite proof is at present still lacking, there is good reason to believe that these fish had come out into deep water during the autumn of the previous year, at the time when they are known to disappear from the surface waters inshore. But where did they spend the ensuing winter? Before providing an answer it is convenient to consider first those other fish which, unlike the majority, do not move outward and westward into deep water in the autumn but spend the winter months on or near the sea bottom in shallower places nearer land—e.g. along the edge of the Hurd Deep some 40 miles south-east to south-south-west of Start Point (Cligny, 1905, 1912; Bullen, 1908), along the southern side of the Vergoyer Bank near Boulogne, and around the numerous small scattered sand banks in the vicinity of Dieppe (Cligny, 1905; Le Gall, 1935). Of the northern fish, numbers sojourn during the winter months on the bottom around the Smalls and Saltees, and are fished from there, particularly by French trawlers (Le Gall, 1928, 1935). At this time these fish are truly demersal and can be caught on the sea floor by commercial trawlers specially equipped for the purpose.

It is not clear what the conditions are that attract the mackerel to certain restricted situations on the sea bed in winter. The only feature that can be detected as common to all of them is an interruption in the level of the sea bed caused by banks or gulleys. There is no uniformity of depth and none of temperature. Mackerel fished along the edge of the Hurd Deep are taken in about 40 fathoms; around the Vergoyer Bank in 12–18 fathoms; in 11–14 fathoms around the Dieppe Banks; and in 30–50 fathoms in the Smalls and Saltees areas. It seems likely that associated with these unevennesses in the sea bed there must be some condition of turbulence—slight perhaps—that is all-important for the mackerel. Although the presence of well-defined mackerel shoals (such as those of the Hurd Deep, Vergoyer Bank and the other localities mentioned) cannot be recorded with absolute precision around the many declivities and acclivities on the floor of the Celtic Sea, mackerel are regularly trawled from various parts of it.

The winter habits of the mackerel, therefore, are now seen to fall into one coherent pattern and the inconsistencies that puzzled earlier writers arose simply through inadequate knowledge. The general statement that the mackerel is a pelagic and migratory fish must be modified. The adult mackerel, at any rate in the English Channel and Celtic Sea, is pelagic and migratory only during a portion of the year. In the other part it is demersal. During the first portion of its demersal period it packs densely in restricted areas and is non-migratory. This was first noted by Cligny (1905, p. 99), who states that these bottom shoals are so dense and so sharply delimited that of two trawlers working side by side one will have a large catch of mackerel and the other none. This is also referred to by Bullen (1908, p. 283), and has been confirmed by old fishermen who participated in some commercially unsuccessful trawling experiments for mackerel from Plymouth.

The fortunes of the fishery reveal that this strongly delimited, densely packed phase of the bottom-living period lasts only for a short time—2 or 3 months at the most. Thereafter the concentration spreads outward in one or more directions from its focal point. In so doing the fish still remain in packs, but of more normal density, the extreme compactness of the first bottom phase having been lost. The Hurd Deep fish, for example, after remaining stationary in a restricted area along its edge until about January, then spread in a north-westerly direction towards Start Point and the Eddystone, where they are caught by French trawlers until the month of March or April.

During the years 1936–39 the Plymouth Laboratory's research ship *Salpa* and a local steam trawler caught 753 mackerel in nine small lots during January–April in an ordinary otter trawl towed very fast on the bottom in the Lizard–Start Point area. The positions of capture (shown as a composite diagram in Fig. 6) of even those few catches indicate a westerly spread of the fish on the sea floor in those early months of the year.

It is during this slow dispersal phase that the change-over from demersal to pelagic habit takes place. Not all at once, but successively, shoal after shoal rises to the surface, and, after they have done so, the spring migration to the spawning ground takes place.

The presence of the Plymouth drift fishery for mackerel off Start Point and the Eddystone in the early months of the year is thus easily understood. The fish that spend the earlier winter months in the vicinity of the Hurd Deep come to the surface in that area and then make their way 'down channel' on a spawning migration to the spawning grounds in the Celtic Sea. Likewise, the fish that winter by the Smalls spread southward across the mouth of the Bristol Channel before rising and continuing their way for some distance parallel to the Cornwall coast and then turn westward to the spawning grounds. On these fish the mackerel drift fishery of the North Cornwall coast in early spring depends. The Saltees fish, and perhaps others that have wintered to the westward of the St George's Channel, spread westward parallel to the Irish coast before rising and turning southward towards the spawning grounds, thus providing the catches close to the Irish coast in the early months of the year (*vide* p. 522).

It seems unlikely that all of the vast mackerel population of the whole south-western area can find room to winter hard by the slopes of the Hurd Deep and the various banks and shoals that have been mentioned. Doubtless some are present also in other inshore places (*vide* Green, 1894, pp. 357–8); but even so, it seems certain that the vast majority must go farther afield to find similarly suitable conditions. This involves a return to the bottom of the Celtic Sea with its numerous banks and knolls, and it is significant that mackerel are regularly caught by British steam trawlers in their vicinity. It may well be that even those slopes also are not sufficient in number and extent

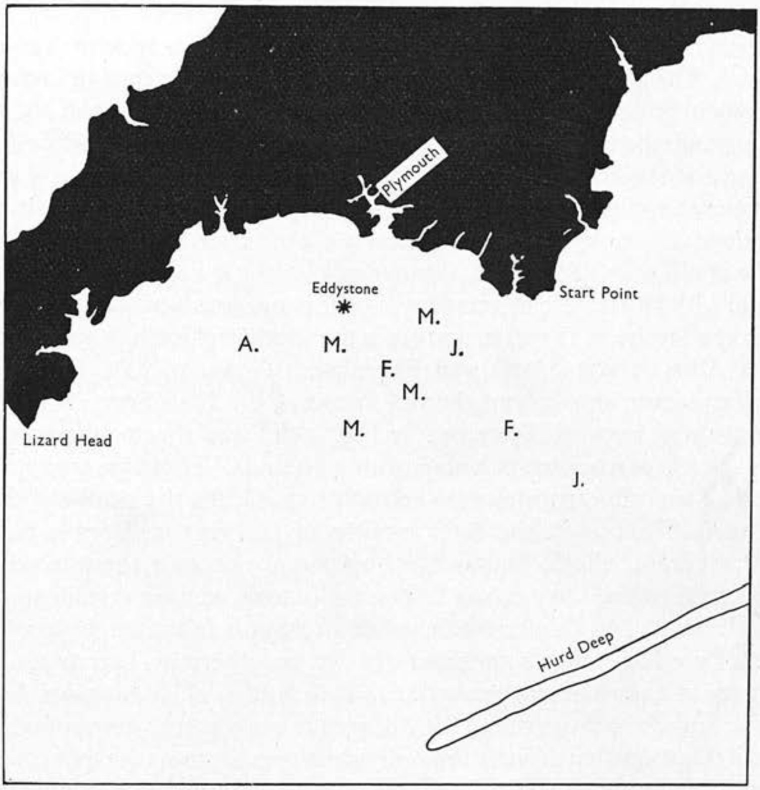

Fig. 6. Chart of area Start Point to Lizard Head. Letters indicate positions in which mackerel were captured on the bottom by two Plymouth vessels during the years 1937–39. J = January; F = February; M = March; A = April.

to accommodate the whole population and that many fish have to seek the declivity of the continental slope in order to pass the winter in the conditions they require. That mackerel should spend the winter months hard by the outer edge of the continental plateau is entirely consistent with their known habit elsewhere of concentrating where there is an interruption in the level of the sea bed.

Although absolute proof is lacking, it appears to be a fully justifiable assumption that these mackerel, acting in conformity with what is now known of their fellows, spread inwards over the outer fringes of the continental plateau in the opening months of the year and then, rising from the sea floor, form part of the great pelagic shoals that migrate eastwards in the Celtic Sea and spawn there in the early spring before continuing their landward journey. In other words, that part of the sea floor from which they approach the spawning ground happens to be to the westward and seaward of it. Other fish, that wintered near other suitable acclivities and declivities nearer the coast-lines, approach the spawning grounds from various other directions at the same time. But the directions in which the shoals are moving are merely incidental. The significant point is that they all have wintered in comparable conditions in widely scattered localities, from the Hurd Deep and the Smalls to the edge of the continental slope at the outer boundary of the Celtic Sea; all rise to the surface in spring and migrate to a common spawning ground, thereafter returning shorewards again and dispersing along the coasts during the summer and autumn; and all, or nearly all, return to the sea floor in winter. How far afield they go in their summer migrations it is at present impossible to decide with any degree of certainty, but it is not improbable that some pass through the Straits of Dover to and from the southern North Sea, as suggested by both Allen (1897, p. 28) and Ehrenbaum (1914, p. 51). Others in all probability spread throughout the full extent of the Irish Sea.

The arrowed lines on the chart in Fig. 5 indicate the movements of the various schools of mackerel to the spawning grounds.[1] These are true spawning migrations, and appear to have no relation to food, for the mackerel that rise to the surface waters in the early months of the year undergo a period of fasting, not from 'choice' apparently, but simply because there is very little available food there. They do not fast on the bottom where a certain amount of food is available, and they break their fast afterwards in the upper layers when opportunity offers—as it sometimes does in an otherwise barren sea by the appearance of a shoal of small pelagic fish such as *Maurolicus pennanti*. Amongst samples of mackerel from the Celtic Sea area in early spring, most of which are fasting, it is not unusual to find a few individuals whose stomachs are packed with those small fish, as many as thirteen having been counted in a single stomach.

Of the 753 mackerel caught between 1936 and 1939 on the bottom between Lizard Head and Start Point (p. 528) 67 % contained considerable quantities of food consisting chiefly of small fish and Euphausiids (*Nyctiphanes couchii*).[2] On the other hand, 600 pelagic fish caught by drift net in the Celtic Sea in the months of March[3] during those years contained food in only 43 % of the stomachs and then only in very small quantities, apart from a few individuals that had gorged themselves with *Maurolicus pennanti*.

[1] Broken lines indicate movements that are as yet presumed and not proved.

[2] One stomach contained seventy-three individuals of this species plus unidentifiable crustacean remains.

[3] No drift net samples were examined in January and February.

Over the course of one full year, therefore, the life of most adult mackerel in the south-west region appears to fall into two main periods, a demersal period and a pelagic period, with a brief transition period during which the fish return to the bottom and reform shoal.[1] This can conveniently be summarized as follows:

1. DEMERSAL PERIOD

(i) *Compact phase*

Intensely dense and extremely circumscribed concentrations of fish massed on the sea floor in very localized positions distributed over wide areas.

November, December

(ii) *Deployment phase*

Concentration diminishes; still keeping to the bottom the fish spread slowly outwards over adjacent areas before ascending to the upper waters and giving rise to pelagic shoals.

December, January, February

2. PELAGIC PERIOD

(iii) *Shoaling phase*

Active migration of the shoals to the spawning grounds and return (or continuation) shorewards.

January–July

(iv) *Dispersal phase*

Shoals broken up and fish dispersed in inshore waters around all coasts.

June–October

3. TRANSITION PERIOD

(v) *Reconcentration phase*

Disappearance from surface waters and return to phase (i).

October, November

During phase (ii)—the deployment phase—the fish appear to perform small diurnal vertical movements, rising from the sea floor during the night and descending again during the day. Trawling during this phase is therefore most successful during daylight hours (Bullen, 1908, p. 283).

DISCUSSION

In the light of this new information concerning the habits and migrations of adult mackerel in the south-western region it is instructive now to examine what is known of their movements and behaviour in other places.

[1] These changes do not take place everywhere simultaneously, so there is no period of the year during which at least a few scattered schools of pelagic mackerel cannot be found.

With regard to mackerel in all the European seas Allen (1897, p. 25) makes the general and comprehensive statement that 'the first approach of the mackerel to the coast in spring or early summer is for the purpose of spawning' and adds the interesting comment that 'the advantage to the species of the young fish being hatched out near the shore where the smaller forms of pelagic organisms are present in abundance and the plankton is increased by the numerous larval forms of those species which inhabit coastal waters, is obvious'.

With special reference to the Celtic Sea and the English Channel area Allen (1897, pp. 12, 17) mentions the presence of fish 30–40 miles from land between Start Point and Plymouth in the months of January to March, at the same time giving the end of March or early April as the time of the approach of the main shoals 'towards the southwest coasts of Ireland and the west coast of France'. He makes no attempt to explain the presence of mackerel so far up channel in winter and early spring while the main shoals are still far away to the westward. Ehrenbaum (1914, p. 13) also states that the great majority of English Channel mackerel appear to arrive in early spring from the adjacent waters of the Atlantic. He attempts to explain the presence of mackerel far up the channel long before the main shoals arrive by suggesting that 'the mackerel sometimes move, in great numbers, still keeping to deep water, far eastward, into the Channel', before rising to the surface. This author, too, believed that mackerel everywhere move in towards the coasts in spring to spawn (1914, p. 17) and gives the months of May, June and July as 'the true spawning time' in both European and North American waters. Much emphasis is placed upon this uniformity of spawning in such widely distant regions. Only in the Mediterranean is the spawning time stated to be 2 months earlier. In a footnote Ehrenbaum (1914, p. 75) makes only passing reference to an important statement by Rathbun, quoting Hardin (1896, p. 81) who found in the New York market mackerel taken on the 17 April some 65 miles south-east of Cape Henry, that were already spent. This observation is possibly of much more importance than Ehrenbaum attaches to it and may indicate much earlier spawning than has been ascribed to mackerel in those waters (cf. p. 535, *infra*).

Meek (1916, p. 320), also in a general statement embracing all mackerel (*Scomber scombrus*), says that 'the spawning migration is an anadromous one', that the season is May to July, and that spawning takes place when they arrive in coastal water (*op. cit.*, p. 326).

Although, as we now know, these general statements concerning the mackerel do not hold good in the English Channel and Celtic Sea, it is significant that, in the North Sea, they are partly true. In that area by far the largest number of mackerel eggs have always been found on the Norwegian side of the Skagerrak very close to the south coast of Norway (Ehrenbaum, 1914, p. 18), and at its inner end off the Swedish coast from Väderöfjord to Hallö and Paternoster 'and thence diagonally across to the Skaw' (Ehrenbaum, 1923, p. 11). Here, without doubt, is a shoreward migration to spawn, chiefly in the months of May, June and July. But it should be noted, by reference to a chart of the eastern North Sea, that *although the migration is shoreward from adjacent offshore waters, it is at the same time a migration from shallower water to the vicinity of the 100-fathom contour.*

There is thus a very close similarity between what we now know to be the chief spawning locality of the south-western region and that of the North Sea area. Both lie close to the 100-fathom line. In both areas this contour closely follows the edge of a well-marked slope in the sea bed from shallow to deep water—i.e. to the depth of the Atlantic Ocean in the Celtic Sea; and, in the Skagerrak, to the lesser but, nevertheless, considerable depths (over 400 fathoms) that are present there and which are not found anywhere else in all the North Sea region.

There is the further similarity that mackerel eggs are found, but in much smaller numbers, widely distributed over adjacent parts of the North Sea and the Kattegat (Buchanan-Wollaston, 1911, p. 218). Ehrenbaum has shown that in the North Sea, too, during the colder season of the year, from November till about May, great numbers of mackerel are present on the bottom chiefly around the Great Fisher Bank and northwards to the Viking Bank along the edge of the Norwegian Channel (1912, p. 4; 1914, p. 36). He also points out that the trawl catches of these fish over the different months of the year 'seem to indicate that the mackerel taken in winter are for the most part identical with the shoals which in spring appear on the coasts of the North Sea and Skagerrak in order to spawn' (1914, p. 36).

What we now find, therefore, is that after spending the winter months on the sea floor in the vicinity of the slopes produced by banks and gulleys, the mackerel in both the North Sea and south-western areas migrate to certain restricted spawning grounds in the vicinity of the 100-fathom line. It so happens that in the North Sea this contour lies close to the Norwegian and Swedish shores. This brings about the anomalous result that mackerel migrating from the shallow waters of the North Sea to spawn in the deep waters of the Skagerrak, and, to a lesser extent, in other Norwegian Fjords farther north, are, nevertheless, at the same time also migrating shorewards. That is to say, that most of the mackerel in the North Sea, like their brethren in the English Channel and Celtic Sea, migrate from their winter quarters to deep water to spawn; that in the North Sea this deep water happens to lie close in by the shore whereas in the south-western region it lies far out in the Celtic Sea, a long way from the land.

It is this apparent anomaly that hitherto has led to such confusion in trying to interpret the migrations of the mackerel. The coincidence that the deep water they favour happens, in the North Sea, to lie hard by the land, and that this was the first spawning ground to be investigated has given rise to the belief that all mackerel migrate shorewards to spawn. The fact that mackerel eggs are never found except in comparatively small numbers near the shore around the south and west coasts of England should have led to at least a suspicion that this did not hold good there. But with only one remarkable exception this suspicion seems never to have arisen in anyone's mind. The exception was a very enlightened fisherman, Matthias Dunn of Mevagissey, Cornwall, who, in 1893 (p. 3), stated quite definitely that the spawning grounds of the mackerel in the south-west region 'are in those waters covering the plateau of ground within the two-hundred-mile limit of our western and south-western shores, known to our sailors as about or within soundings'. This remarkably accurate statement is not even mentioned, so far as I can ascertain, by any subsequent investigators. Perhaps they had never come across it; or perhaps (more likely) they considered it to be too preposterous for serious consideration. Day (1880–84, p. 85), however, appears to have retained an open mind on the subject, for he says that at certain seasons mackerel approach the shores in countless multitudes 'either prior to, during, or after breeding'.

Respecting the migrations of the mackerel on the western side of the North Atlantic there existed for a long time two very well-defined schools of thought. One held that the mackerel undertook extended migrations both to and from deep water well offshore, and also along the shore, when this was reached, in a south to north direction (Brown Goode, 1879, p. 63). Other investigators and observers (quoted by Brown Goode, 1879, pp. 56 *et seq.*)[1] held that the mackerel spent the winter on the sea floor, not very far from their summer haunts, where they lay in a comatose state either on or even partly embedded in the bottom mud or sand. These apparently opposing views were, in fact, held by American and Canadian workers respectively and were fiercely debated in a controversy concerning American rights to fish in Canadian waters. The American argument was that, since the shoals moved northward from American to Canadian waters, American fishermen were entitled to follow them thither. The Canadians held that, on the contrary, such migrations did not take place and opposed the American claim to a right to fish in their waters.

Each side provided some useful evidence in support of its claim. The American view was supported by the northward movement of the fishery. Canada depended mainly on rather fanciful 'eye-witness accounts' of mackerel being seen on the bottom in a torpid state in winter months, and on the more reliable fact that mackerel occasionally could be caught by nets on the bottom near the shore in winter. Brown Goode himself (1884, p. 102) more or less admits the claim that mackerel are not infrequently found in the stomachs of cod and halibut taken on and near the bottom on George's Banks in the winter season, and Collins (1883, p. 274) reported that in late February, 1882, many mackerel were taken in the stomachs of cod that had been caught near bottom some 10 miles off Egg Harbour, N.J., in 12–15 fathoms of water. Summing

[1] The very early Canadian publications by W. F. Whitcher and Henry Youle Hind have not been available to me for direct consultation.

up, Brown Goode conceded rather grudgingly that 'it is by no means demonstrated that certain schools of mackerel do not remain throughout the year in waters adjacent to the coasts of Canada' (1884, p. 96). Nevertheless, he considered such cases to be quite exceptional and held firmly to the conviction that the weight of available evidence was overwhelmingly in favour of those who held that the mackerel make extensive migrations along the coasts, in addition to returning to deeper parts of the ocean on the approach of winter.

As more information became available, however, the views of both parties became so modified that Bigelow (1925, p. 192) was able to state that 'scientific opinion has gradually crystallized to the effect that the essential features of the seasonal migrations of the mackerel are essentially a spawning journey inshore and into shallow water in spring alternating with an offshore movement combined with a descent into deep water in autumn'. He then adds that, according to geographic conditions, these 'fundamental changes of situation' are accompanied by horizontal journeys of greater or less length and in various directions. According to this author (1925, p. 206) mackerel spawn off the North American coast from the latitude of Cape Hatteras (35° 15′ N.) to the Gulf of St Lawrence, where the heaviest spawning along the whole coastline takes place, closely followed by the Gulf of Maine, especially in the Massachusetts Bay area. In the latter region the chief spawning season is said to extend over the last half of May and the month of June; in the Gulf of St Lawrence spawning activity reaches its maximum a month later in the latter half of June and the first two weeks of July.

Although exact comparisons are impossible because of the different methods and gear used for collection, it may be significant that the records of mackerel eggs obtained in both those regions (Bigelow, 1925, p. 206; Dannevig, 1918, p. 8; Sparks, 1929, pp. 445–450) reveal widespread distribution of eggs in comparatively shallow coastwise waters in numbers that appear to be comparable with those obtained by Corbin in the Celtic Sea to landward of the main spawning centres after maximum spawning intensity had passed. If this indeed be so, much importance must be attached to Bigelow's further statement (1925, p. 207) that, in the Gulf of Maine region, egg records from offshore localities, though extremely scanty, nevertheless clearly indicate that spawning takes place in the vicinity of some or all of the many banks that lie well offshore and over deep water[1] as well as in the shallow coastwise waters of the inner parts of the Gulf.

The evidence so far available, therefore, appears to point very strongly to the probability that the habits and migrations of the mackerel on the western side of the North Atlantic will, on further investigation, be found to be very

[1] Bigelow appears here to be referring to depths of less than about 180 fathoms, the deepest soundings found in the various deeps and basins of the Gulf of Maine which is the oceanic bight between Cape Cod and Cape Sable. He adds (1925, p. 209) that 'there is no reason to suppose that they ever breed outside the continental slope', the edge of which, in that region, follows more or less closely the 200-fathom contour.

similar to those of their European kin around the south-west of England and in the North Sea. The existence of hitherto undiscovered, restricted spawning centres of high spawning intensity, probably in the vicinity of the 100-fathom line perhaps as early as April in both the Gulf of Maine and the Gulf of St Lawrence, seems highly probable; and examination of the charts of the two regions suggests that they are well suited to the needs of the mackerel as revealed by our recent researches in the English Channel and Celtic Sea.

Although the migrations of the adult mackerel in the English Channel and Celtic Sea have now become clear, the migrations of the young and immature fish are still obscure, but mention must be made of what little we do know concerning them. Corbin (1947, pp. 73–76) has shown that the larval and post-larval stages, as would be expected, are numerous on the spawning grounds for a short time after the eggs have hatched out; thereafter, they disappear from catches and little is known concerning them. During our investigations the largest post-larva captured in these waters was 21 mm. in length caught in the month of June.

But small mackerel, of from about 13 to about 17 cm. in length, appear in some years in bays, harbours, and estuaries around the south-western shores of England for a short period in early autumn. In 1926 small fish appeared in Plymouth Sound in August and several were caught in sprat nets, their size ranging from 13·0 to 17·2 cm. in length (mean length of all fish 15·3 cm.). In 1927 small mackerel again appeared in the bays and estuaries around the Devon and Cornwall coasts. Fifty of them caught in a sprat seine during August had a mean length of 13·6 cm., the total range being 12·5–15·2 cm. In 1937, 273 small mackerel caught at Newlyn on 4, 6, and 7 August had a length range of 8·0–16·4 cm. with a mean length of 12·7 cm. Those fish first appeared in the middle of July and remained inshore until nearly the end of September. They were present in very large numbers—so much so that reports of their presence in such abundance were at first disbelieved. Many Newlyn fishermen were very definite in their assertions that they had never seen mackerel of such small size before.

Their appearance, in fact, in inshore waters in this region, takes place only at long and irregular intervals. Nor are they found with any greater frequency elsewhere in British waters. The Scottish Fishery Board[1] records the capture of small mackerel on the bottom in a small-meshed covering of the cod end of an otter trawl in September and November 1929; September and October 1930; September and October 1932; August, September and October 1933; August 1935; and in September 1936.

There are no records in the Board's log-books of any catches of these small sizes in 1927, 1928, 1931, 1934 and 1937.

The capture of small mackerel is not to be expected in an uncovered trawl, but Hickling,[1] while fishing for hake off the west coast of Ireland, has come across them in the stomachs of hake and certain other fishes. Ehrenbaum

[1] Private communication.

(1923, pp. 19 *et seq.*) gives details of the capture of small mackerel in the North Sea by several workers of different nationalities in the late summer and autumn. Malm (1877, p. 409) mentions a great shoal of small mackerel that appeared in the Skagerrak, near Christenburg in the Gullmarfjord, on 27 July 1872. They were so small that they all escaped through the meshes of ordinary seines and only ten could be obtained for examination. These fish were between 67 and 100 mm. in length. To the fishermen of the district such small mackerel had until then been entirely unknown so that, as on the Channel coast of England, they must arrive only on rare occasions at long intervals.

From the information available, therefore, meagre and incomplete though it be, it is evident that juvenile mackerel, like the adults, are present at times on the sea floor and at other times in the upper layers of the sea. Their appearance in some years in huge numbers in inshore waters for a few weeks in summer and early autumn reveals that they also carry out migrations, but the fact that they do not appear around the shores every year suggests that those migrations, in the main, are less extensive and less regular than those of the adult fish.

One cannot but conclude, therefore, that the migratory behaviour of young mackerel may be very similar to that of the adults; that they seek bottom in the late autumn and winter and rise again to the upper layers in due season. As they so seldom come inshore, it would appear that their horizontal migrations are, as a rule, less extensive than those of adult fish. As they grow and approach maturity, those migrations must approximate more and more closely to those of the adults until at last, when they reach maturity, they join the spawning shoals and migrate with them.

Summary

In the English Channel and Celtic Sea mackerel spend the winter months on the sea floor densely packed in places where its level is interrupted by banks and gulleys.

In the early spring the fish rise to the surface and migrate to a common spawning ground that lies far out to the westward of the Scilly Islands in the vicinity of the 100-fathom contour.

The very localized positions in which mackerel spend the winter are widely distributed throughout the area in both deep and shallow water. Large schools of migrating fish converge upon the spawning ground from many directions, therefore, in the spring for spawning.

Fish that have wintered near the land must migrate *offshore* to reach the spawning ground; those that spend the winter on the bottom to seaward of the spawning ground must migrate *shorewards* to reach it. Off the south-west of England there is no single shoreward migration to spawn in shallow water as has previously been thought.

In the North Sea the chief spawning grounds of the mackerel are also near the 100-fathom contour which, in that region, happens to lie very close to the land

in the Skagerrak and along the Norwegian coast. The chief spawning migration of the North Sea mackerel is therefore towards the coast from offshore localities. This migration is, at the same time, chiefly from shallow to deeper water.

Existing information concerning the mackerel populations on the western side of the North Atlantic points to the probability that their spawning habits and migratory movements do not differ greatly from those of the mackerel in North European waters.

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[1] See footnote, p. 534.

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CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL *SCOMBER SCOMBRUS* L.

II. A STUDY OF THE FISHERY IN THE SOUTH-WEST OF ENGLAND, WITH SPECIAL REFERENCE TO SPAWNING, FEEDING, AND 'FISHERMEN'S SIGNS'

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Zoologist at the Plymouth Laboratory

(Plate I and Text-figs. 1–6)

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Introductory Survey

In a previous paper (Steven, 1948), brief accounts are given of three distinct mackerel fisheries that at one time existed in the south-west of England—an inshore fishery in the English Channel carried on from Plymouth, a deep-sea fishery from Newlyn, Cornwall, and an inshore fishery from Newlyn and some other Cornish ports. One of these fisheries, the Plymouth one, no longer exists. After a few years of considerable activity following the termination of the 1914–18 war, this fishery collapsed in 1924 (Table I) and came entirely to an end a few years later. The small quantities of mackerel landed at Plymouth in subsequent years have been incidental catches by vessels fishing for herrings or pilchards.

The Cornish inshore fishery took place mainly at no great distance to seaward of the northern shore of the Devon-Cornwall peninsula and was carried on chiefly by small local craft, both wind- and motor-driven; but a number of visiting east-coast drifters used also to participate, especially during January and February, when stormy weather prevented their going very far to sea in search of other shoals in deeper waters beyond the Scilly Islands (Steven, 1948,

p. 520, fig. 3). Soon this fishery too fell upon hard times and the small local craft gradually abandoned mackerel fishing. In 1931 the local Fisheries Officer reported to the Cornwall Sea Fisheries Committee that, so far as local vessels were concerned, the fishery had arrived almost at the point of extinction.

The failure of both the Plymouth and Newlyn inshore fisheries was due to a decline in the quantity of fish in nearby waters, combined with low prices which made small catches unremunerative. The fall in fishing yield in those years is clearly reflected in the mean weight of fish per landing by the local vessels engaged in the Newlyn fishery. At no time[1] from 1906 (when reliable returns first became available) until 1927 did this average fall below 10 cwt. (Text-fig. 1), and was generally much higher. But with the single exception of 1928 the 10 cwt. figure was never again reached; in fact the individual

TABLE I. QUANTITY OF MACKEREL LANDED AT PLYMOUTH, 1919–38 INCLUSIVE (IN CWT.)

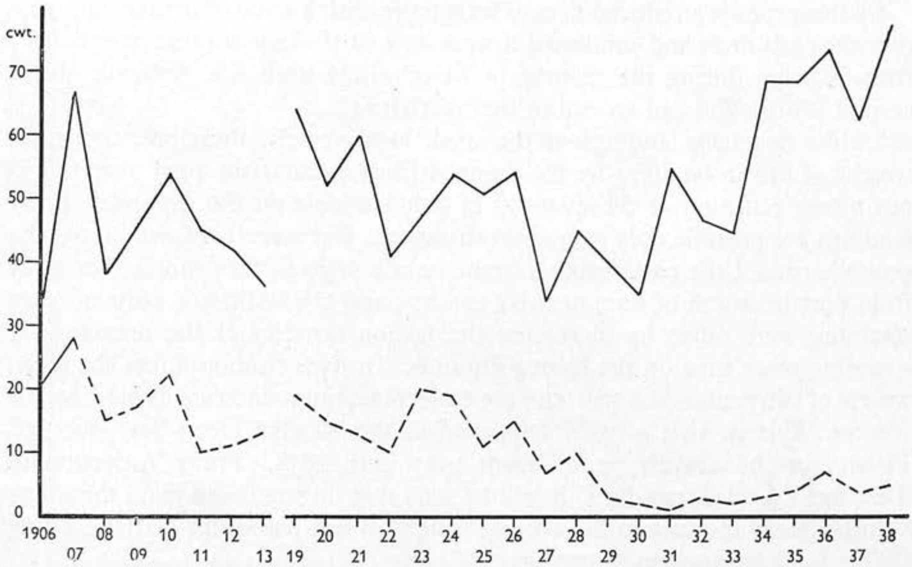
Year	Quantity	Year	Quantity	Year	Quantity
1919	15,521	1926	4080	1933	2200
1920	33,618	1927	3080	1934	1859
1921	18,117	1928	2582	1935	2401
1922	18,198	1929	3005	1936	2670
1923	15,551	1930	3109	1937	1669
1924	5,366	1931	3101	1938	1156
1925	5,229	1932	4709		

landings were generally less than half that amount. These weights are a reasonably accurate index of the quantity of fish available on the fishing grounds because landings by local vessels represent only one night's fishing.

Many of the steam drifters reacted to the decline in the inshore fish stocks by postponing their arrival in Newlyn until about the beginning of March in each year, when weather conditions permitted them to proceed at once to more distant fishing localities in the open sea well beyond the Scilly Islands, where better catches were to be had on different bodies of fish migrating in from the westward. But even as late as 1930 some steamers still endeavoured to obtain satisfactory catches in nearby localities in January and early February, but without success, and they worked at a loss until better weather in March enabled them to proceed to the distant grounds where better results were obtained. This was the very last year in which steam drifters fished from Newlyn as early as January. Since that time the steam-drifter fishery has opened invariably on the deep-sea grounds not earlier than the last days of February or the first days of March. But even the deep-sea grounds failed to provide satisfactory returns for all the participating craft and many of them gave up mackerel fishing altogether (Table II), their numbers falling from 90 in 1920 to 23 in 1940, the last year of normal fishing.

[1] War years excepted.

The steam drifters that did not give up fishing strove to maintain their catches at remunerative levels by working at ever increasing distances from land until eventually, from about 1927 onwards, it became the regular custom of most of the fleet to open the fishery every spring on grounds as much as 100 miles or more to seaward of the Bishop Rock (Scilly Islands) on bearings lying generally between W.N.W. and W.S.W.



Text-fig. 1. Mean weight in cwt. of mackerel per landing at Newlyn in the years 1906–38 inclusive: (——), by steam drifters; (- - - -), by local craft.

TABLE II. NUMBER OF STEAM DRIFTERS FISHING FROM NEWLYN IN THE YEARS 1920–40 INCLUSIVE

Year	No.	Year	No.	Year	No.	Year	No.
1920	90	1926	82	1931	47	1936	31
1921	60	1927	74	1932	43	1937	23
1922	80	1928	60	1933	43	1938	27
1923	80	1929	55	1934	35	1939	25
1924	68	1930	52	1935	34	1940	23
1925	87						

Daily landings from these distant grounds obviously became impossible, so the practice of preserving the fish in ice was extended and improved to enable the ships to stay at sea for more than one night at a time on each fishing trip. Single landings at the beginning of the season, therefore, came to represent as many as 4 nights' fishing.

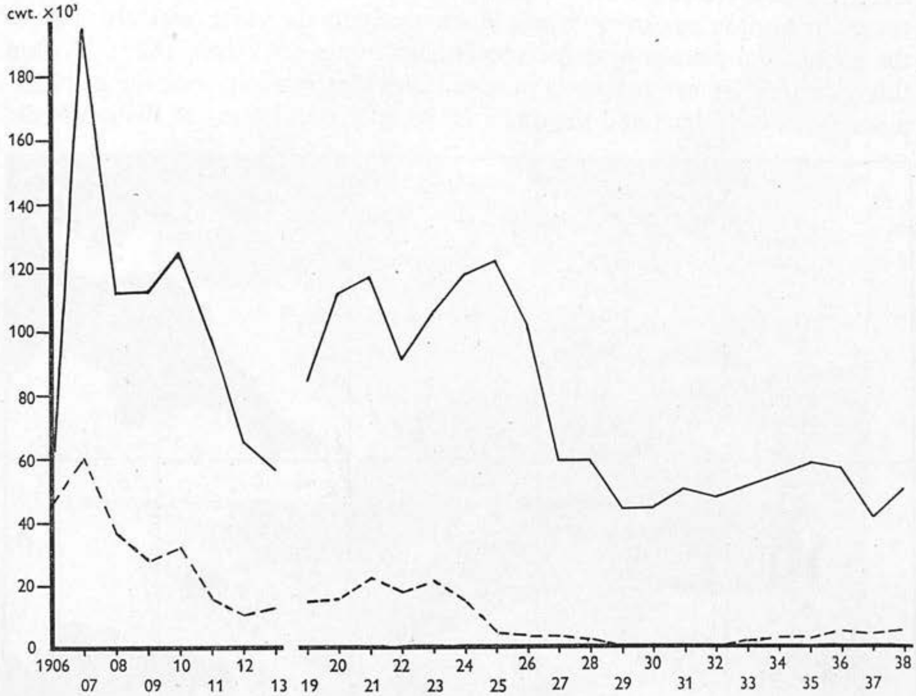
At the same time the fishing capacity of each drifter was also undergoing an important change. Before the war of 1914–18 the nets used by those craft were of a type known as 'fly nets' and had a standard size of about 20 yd. length and 5 yd. depth. On resumption of fishing after peace returned a larger 'footrope net' began to be introduced which is about 33 yd. long and just over 6 yd. deep. By about 1933 the old type had been almost entirely replaced by the new. The number of nets in each fleet remained unchanged at approximately 180. The fishing area of each drifter's fleet of nets was therefore almost exactly doubled, rising from approximately 18,000 sq.yd. to approximately 36,000 sq.yd.

By these means a reduced fleet of little more than a score of drifters was able to make ends meet and continued to operate a small deep-sea mackerel fishery from Newlyn during the months of March–June until the outbreak of the second World War put an end to their activities.

Unlike the daily landings of the small local vessels, therefore, the mean weight of fish in landings by the steam drifters from about 1927 onwards, is not a true reflexion of the quantity of fish available on the grounds. Daily landings are possible only over short distances. But scarcity of fish on nearby grounds caused the participating steam vessels to go farther and farther away from port in search of remunerative catches, and the additional costs of extra steaming were offset by increasing the fishing capacity of the nets and by spending more time on the fishing grounds. In such circumstances the mean weight of fish per landing will tend not to decrease but to increase as fish become scarcer. This is what actually happened in the Newlyn Deep-Sea Mackerel Fishery in the 12-year period from 1927 until 1938. From inspection of Text-fig. 1 (and Appendix I) it will be seen that during those years there was a fairly steady increase in the average weight of fish per steam-drifter landing from 34 cwt. in 1927 to 78 cwt. in 1938.

There was no corresponding increase in the total yield of the fishery. This, in fact, from 1927 onwards, remained remarkably constant (Text-fig. 2), because, although the mean weight per landing increased, the number of landings decreased. This decrease in the number of landings was due only in part to the increased length and duration of the fishing trips. Another and more important cause was a gradual decline in the public demand for mackerel. This is indicated by their market value on first sale (Table III), which fell steadily from 19*s.* 5*d.* per cwt. in 1929 to only 9*s.* 11*d.* in 1936. There was a slight recovery to 13*s.* 8*d.* in 1937, but another fall to 12*s.* 4*d.* in 1938.

More mackerel could have been landed by the existing fleet if the demand for them had existed; for from about 1930 onwards the skippers of steam drifters working from Newlyn voluntarily agreed from time to time to stay in port for from 1 to 3 days after each landing in order not to cause a glut of unwanted fish on a sluggish market. In some years approximately 20% of possible fishing time was lost in this way. The Statistical Tables of Sea Fisheries in England and Wales contain data covering the total landings of mackerel at Newlyn and the total number of landings by the different kinds of vessels, but no information is given either with the Tables or in the Official Reports (1906–38) concerning such changes in the fishery as have been briefly described above. Unfortunately, therefore, the official statistics concerning the Newlyn deep-sea fishery for mackerel have little or no biological significance. Important



Text-fig. 2. Total landings of mackerel at Newlyn (in thousands of cwt.) in the years 1906–38 inclusive: (——), by steam drifters; (- - - -), by local craft.

TABLE III. AVERAGE VALUE OF MACKEREL PER CWT. IN ENGLAND AND WALES FOR THE YEARS 1919–38 INCLUSIVE[1]

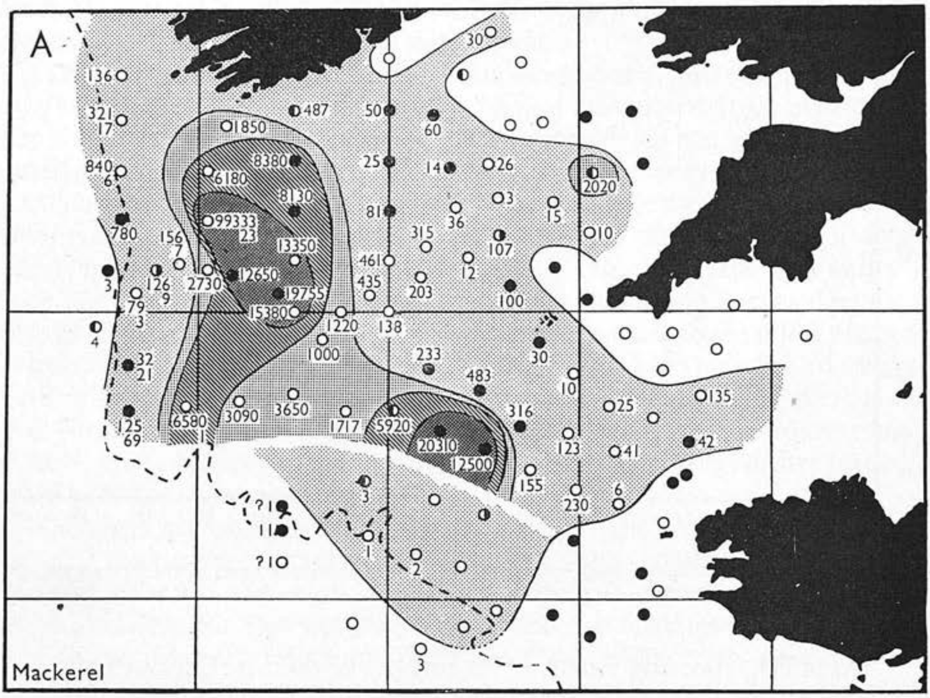
Year	Value	Year	Value	Year	Value	Year	Value
1919	39*s*. 10*d*.	1924	17*s*. 9*d*.	1929	19*s*. 5*d*.	1934	11*s*. 3*d*.
1920	15*s*. 1*d*.	1925	16*s*. 4*d*.	1930	17*s*. 9*d*.	1935	11*s*. 7*d*.
1921	21*s*. 6*d*.	1926	17*s*. 1*d*.	1931	14*s*. 7*d*.	1936	9*s*. 11*d*.
1922	16*s*. 9*d*.	1927	19*s*. 5*d*.	1932	13*s*. 9*d*.	1937	13*s*. 8*d*.
1923	15*s*. 10*d*.	1928	17*s*. 2*d*.	1933	12*s*. 3*d*.	1938	12*s*. 4*d*.

[1] From Statistical Tables of Sea Fisheries.

factors other than the availability of fish on the fishing grounds have greatly influenced both the number and size of individual landings and the total yields—factors that have not been taken into consideration during the compilation of the tables nor recorded with them.

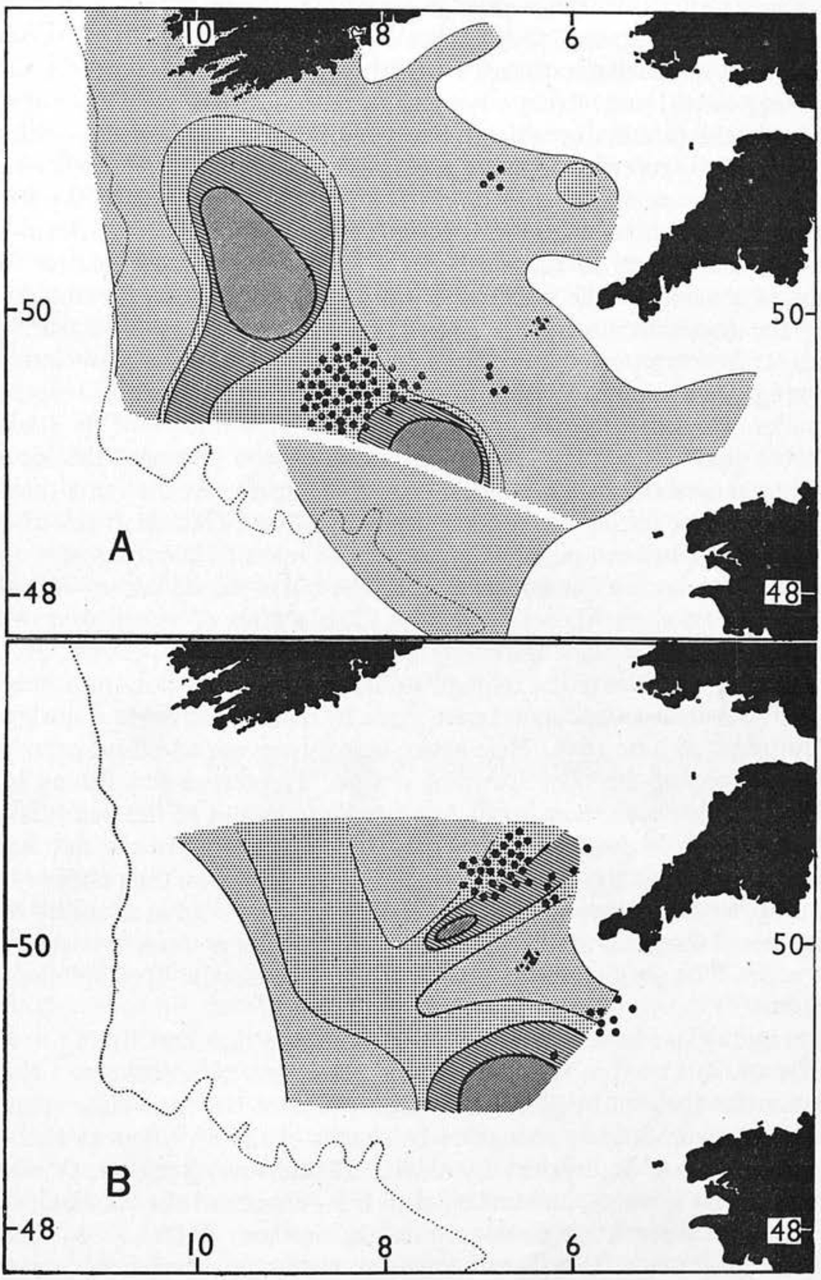
Position of the Fishing Grounds in Relation to Spawning Areas

The Newlyn deep-sea fishery takes place on fish that are moving landwards from the west. While still far off-shore most of them spawn. Heaviest spawning occurs in April in an extensive area of sea overlying the outer (seaward) part of the continental plateau near the 100-fathom contour (Corbin, 1947). Within this area there are two centres of maximal spawning intensity, one lying 40–100 miles south of Ireland and the other 50–80 miles south-west of Bishop Rock.



Text-fig. 3. Distribution of mackerel eggs (1–1000; 1001–5000; 5001–10,000; > 10,000) and young stages in the Celtic Sea in April, 1938. Reproduced from Corbin, 1938, p. 74. For further explanation see text.

The general shape and extent of those spawning areas in April 1938—a typical year—are clearly shown in Corbin's fig. 5A (1947, p. 74) reproduced here as Text-fig. 3 (except for the omission of a coloured patch over the western-most stations where young stages were recorded). The numerals in general refer to numbers of eggs, taken in half-hour oblique hauls with the 2 metre stramin trawl by the method described by Russell (1930, 1935). Some, however, attached to the westernmost stations, refer to the planktonic young stages—such as the lower of a pair, or single numbers outside the egg limit (*vide* the original for more exact details).



Text-fig. 4. Mackerel spawning grounds and the locus of mackerel fishing by Newlyn-based steam drifters: (A), in April, 1938; (B), in May-June, 1938. Stippling indicates density of mackerel eggs, as in Text-fig. 3.

Corbin's charts of the spawning ground for 1938 are copied in Text-fig. 4 with the number of eggs and young stages omitted, but having inserted upon them the positions in which ten drifters were fishing during the time that the survey was being carried out. Every 'shot' by each of those drifters is indicated by one dot in the position in which it was made. Fishing by those ten selected vessels was fully representative of the activities of the full fleet of twenty-seven vessels. Reference to the chart (Text-fig. 4A) clearly shows that the fishing fleet was at the time concentrating its attention upon a well-defined area between, and slightly to landward of, the two chief spawning centres. This means, of course, that the best catches were to be had there. It is remarkable, to say the least, that mackerel fishermen should so unerringly have found this particular fishing ground though quite unaware of the presence of any intensive spawning nearby, especially as these grounds lie right out in the open sea 130 miles or more from port.

Corbin (1947, p. 72) has shown that as the season advances the locus of spawning moves eastwards and decreases in intensity. At the same time the locus of greatest fishing activity also moves eastward (Steven, 1948, p. 523, fig. 4). It has not been possible in any year to make frequent surveys of the spawning areas at brief and regular intervals, but a second survey was made during the period 31 May–5 June 1938. The centres of maximal spawning were then in the positions shown by the dark stippling in Text-fig. 4B. On this chart the activities of the fishing fleet are also shown by dots indicating the positions in which actual 'shots' were made by representative ships during the first fortnight of June 1938. Here again, best fishing was found near the landward periphery of the chief spawning centres. The reason why fishing is not concentrated between them, as in April, is the presence of the Scilly Islands and the 'toe' of Cornwall in the very place where, in their absence, best fishing would be expected; for since good catches are obtained on the periphery of a spawning centre, the very best results of all should be found in a locality which forms part of the peripheries of two separate spawning grounds overlapping at their edges. The position of the highest fishing intensity in April fulfilled this condition.

It is quite clear from the fishing fleet's activities that best fishing is to be found near, but not on, the centres of maximal spawning intensity. No explanation for this can be given. The most probable reason is either that the fish do not swim actively enough to be caught in the drift nets or that they remain too deep to be reached by them. Ehrenbaum (1923, p. 5) records that Holt, in a private communication to him, expressed the conviction that mackerel in full spawning do not rise to the surface. Collins (1883, p. 277) also states that mackerel in North American waters sink during the season of reproduction and rarely appear in shoals at the surface. It should now be possible to obtain definite information on this point by investigating the spawning centres and fishing grounds with a suitable echo-sounder. Unfortunately, none was available on any of the ships with which these researches in the Celtic Sea were carried out. Arrangements are now being made for echo-sounder surveys to be carried out as soon as circumstances permit. Until this is done one can do no more than note the possibility that while spawning in deep water the fish may be either deep or relatively quiescent, or even both.

Since the fishing fleet does not catch spawning fish in the first part of the season, very few ripe mackerel arrive on the fish markets during the months of March and April. It is not until May and later that appreciable numbers of fish containing small quantities of ripe ova and sperm are landed. The explanation for this appears to be that those fish that have not yet completely spawned are now in much shallower water and cannot go down very deeply to do so. The result is that some spawning fish can now be taken in drift nets on fairly active spawning centres even though best fishing is still to be had on the periphery of such centres.

When the two inshore fisheries existed they depended on unripe fish that were in the first stages of migration to the spawning ground, i.e. they, too, worked on non-spawning populations.

Having spawned off-shore, the mackerel perform a return migration to the coast (Steven, 1948, p. 524). This return migration is not, therefore, a spawning migration as has been supposed for so long. It is simply a post-spawning anadromous migration during which the fish are actively feeding; nevertheless it cannot be said that they come inshore *in order* to feed.

The Spawning of the Mackerel

Spawning takes place throughout the Celtic Sea during the period March till July. It increases very rapidly in intensity after the start, and by mid-April reaches a peak which lasts until May. Thereafter it decreases, until by the end of July it is only very slight. In the English Channel and also in the Irish Sea this slight residual spawning continues until August and even, in some years, until September (Corbin, 1947, p. 71).

This long-drawn-out spawning season is due, in part at least, to the fact that various populations of mackerel, converging on their off-shore spawning grounds from different winter quarters, both near and far away, do not all arrive there at the same time. When spawning activity is at its greatest—in the western part of the Celtic Sea in April—fish that wintered in the English Channel are still on their way westward (Steven, 1948, p. 520, fig. 3), and not yet fully ripe. It seems possible that this spread-over may be related not only to the different lengths of the migratory journeys but also to differences in the environmental conditions, particularly of temperature, in which the fish spend the winter. According to Cooper's analysis of such temperature data as exist for these areas (Appendix II, pp. 577–81), the waters over the greater part of the Celtic Sea are isothermal down to about 120 m. and in most years have appreciably higher temperatures than those of the Hurd Deep where many if not most of the Channel mackerel spend the winter. Most of the Atlantic Slope mackerel, however, spend the winter below the 120 m. level but they, too, unless they go very deep indeed—which is unlikely—are subject to warmer conditions than the English Channel population. Observations in 1927 and 1932 reveal that the mean winter temperature along the 150 and 200 m. contours in those years was about 0·9° C. higher than the mean temperature at the Hurd Deep; only at 500 m. in 1932 and at 800 m. in 1927 (position 50° 34′ N.; 11° 17′ W.) were Hurd Deep temperatures reached. Deep-water observations are also available for 1929, but Cooper regards that year as an exceptional one. Atlantic Slope water in that year was, at 200 m. depth, 2·5–2·8° C. warmer than the Hurd Deep; even at 986 m. the Atlantic Slope water was still 0·7° C. warmer. It seems clear, therefore, that mackerel wintering on the floor of the Celtic Sea, and in considerably deeper water at the outer edge of the continental plateau, are normally subjected to appreciably warmer conditions than others that spend the winter in the English Channel. Still others wintering near the bottom in the Smalls and Saltees areas will be also subjected to temperatures at least as low as those of the Hurd Deep.

Mackerel wintering around the various banks, knolls and gullies on the floor of the Celtic Sea, and in considerably deeper water at the edge of the continental plateau, are therefore not only nearer the spawning ground but are subjected to appreciably warmer conditions during their demersal period than others that spend the winter in the English Channel and in the Smalls and Saltees areas. It seems reasonable to suppose, therefore, that it is those fish that spend their demersal period in localities near the spawning ground, where also the warmer conditions prevail, that give rise to the early intensive spawning activity, followed by others from the more distant and also colder winter localities. There is also a possibility (supported by Cooper's theory of cascading waters from the shelf area down the side of the continental slope) that there may be a concentration of planktonic food organisms—chiefly copepods—at considerable depths along certain parts of the slope in February and March, especially in colder winters. Mackerel wintering in such localities, therefore, may also be better nourished (Cooper & Vaux, 1949).

Differences in winter temperatures may also be the factors underlying the later date of maximum spawning intensity on the chief North Sea spawning ground in the Skagerrak. Here (Ehrenbaum, 1914, p. 18; 1923, p. 11) the chief maximal spawning activity takes place a month later than in the Celtic Sea. It may be significant, therefore, that North Sea mackerel spend the winter in the vicinity of the Great Fisher Bank and northwards along the Norwegian Channel at least as far as the Viking Bank where winter temperatures are in general as much as 2–3° C. lower than those found in the Celtic Sea (Appendix II).

Another important factor contributing to the great spreadover of spawning activity in both space and time is that in every individual female the eggs mature in successive batches that are spawned one after the other during an extended period, the exact duration of which is not known. Ripe translucent eggs appear in the ovary distributed widely and irregularly amongst still unripe yellowish ova in earlier stages of development. This gives rise to a peculiar speckled appearance that, for want of a better term, has been called the 'plum-pudding' stage (Le Danois, 1938, p. 22,), of which an illustration is given in Pl. I, fig. 1. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, shows no trace of ripe eggs. Their presence can be ascertained only by opening up the ovary and examining the lumen in which a few ripe eggs will nearly always be found even after any particular batch has been shed. These must, however, be carefully looked for; a quick and superficial glance may easily miss them. An ovary that contained numerous ripe eggs in its lumen, but showed no external evidence of their presence, is illustrated in Pl. I, fig. 2. The existence of ovaries in this condition indicates that the final stages of the ripening process take place discontinuously in successive batches of eggs. Were the process a uniform and continuous one ripe eggs would always be visible externally in smaller or larger numbers throughout the whole period from the time that the first eggs ripen until the ovary is fully spent.

This mode of ripening of the eggs in mackerel ovaries is in marked contrast with the condition found in the herring, where all the eggs that are to be spawned in any one spawning season ripen more or less simultaneously, giving rise to the well-known 'mazy' condition in which large numbers of fully ripe eggs can be obtained from a single female at one time. This condition is never found in mackerel. Only a relatively small number of fully ripe eggs is ever present in a mature female at any time and a condition of easily recognized 'maziness' does not occur.

It was probably a more intimate and accurate knowledge of the ripening process in the ovary of the herring than of the mackerel that led Cunningham to make the misleading generalization (1889, p. 25): that in species of fish that swim in shoals and have pelagic and migratory habits the process of spawning is approximately simultaneous throughout the whole population in a given locality, proceeds very rapidly when once begun, and is limited definitely to one short period of the year. This generalization he wrongly applies to the mackerel in which he says: 'all the reproductive products in a given fish are matured and shed within a short space of time.'

The slightly later observations of Moore (1899, p. 5), however, are completely at variance with Cunningham's findings and in full agreement with the results of the present investigations. Moore draws attention to the fact that, in the same run of fish, individuals in very different conditions of maturity are found. The reason for this he very clearly points out to be due to the fact that 'the mackerel matures only a portion of the generation of eggs at one time', as a result of which the ovary 'becomes spotted all over, both externally and on the internal lamellae with translucent spots due to aggregations of the clear eggs'. This very early description of the 'plum-pudding' stage, and how it arises, appears not to have received from subsequent workers the attention it deserves.

Correlated with the extended spawning period in the female there is, in the male, a correspondingly long period during which ripe sperms are present in the testes. The male differs from the female in that from the time that ripe sperms first appear at the beginning of the season an appreciable amount of ripe sperm is always present until the fully spent condition is reached. As in the female, however, the quantity of ripe sexual products present in a male fish at any particular time is always relatively small. Ripe males are generally present in small numbers in commercial catches before ripe females appear in them (Table IV).

TABLE IV. PERCENTAGE OF FISH (IN COMMERCIAL CATCHES BY STEAM DRIFTERS) IN DIFFERENT MONTHS CONTAINING RIPE SPERM OR EGGS

Figures in brackets are the total numbers examined during three fishing seasons (1937–39).

	Males	Females
March	5·9 (584)	0·0 (570)
April	20·6 (569)	7·9 (625)
May	62·5 (578)	52·2 (554)
June	52·8 (625)	47·6 (464)
July	14·4 (223)	17·3 (185)

It will be seen from the table that the two sexes appear in the catches in approximately equal numbers.

FOOD AND FEEDING

Adult mackerel spend part of each year in winter quarters on or near the sea-floor in the vicinity of banks and gulleys distributed over wide areas from shallow to deep water. In the English Channel, demersal concentrations of mackerel are found hard by the Vergoyer Bank off Boulogne, and by the numerous small sandbanks near Dieppe in only a few fathoms; and along the sides of the Hurd Deep in rather more than 40 fathoms. Elsewhere in the south-western area they occur at various depths in the neighbourhood of the Smalls and Saltees, around various banks and shoals on the floor of the Celtic Sea, and even along the Continental Slope itself, where they are regularly caught by British and other trawlers in depths of well over 100 fathoms 'west of Great Sole Bank' and elsewhere, especially in late February and March.

Amongst the mackerel that winter on the bottom in the English Channel fish with packed stomachs are seldom found. On the other hand, not all of them are empty. The fish, therefore, though not feeding voraciously, are not entirely fasting.

In the Plymouth region 753 mackerel were caught by trawl on or near the sea-floor in the months of January–April during the years 1936–39. Of these 67% contained food consisting chiefly of *Nyctiphanes couchi*, mysids, small teleosts, and crangonids, but various other organisms were also represented (Table V).

It is obvious that while on or near the bottom in the English Channel the mackerel were feeding on such organisms as were suitable and available to them. By contrast, the stomachs of mackerel caught in drift nets near the surface in January have been almost entirely devoid of food. A few (just under 5% of the 138 fish examined) have contained traces of phytoplankton embedded in mucus and very occasionally traces of planktonic crustacea (copepods) have been present. Rather more plant material appears in the stomachs in February

TABLE V. PERCENTAGE OF BOTTOM-CAUGHT FISH (PLYMOUTH AREA) CONTAINING IN THEIR STOMACHS ONE OR MORE OF THE ORGANISMS LISTED BELOW

Name of organism	Percentage of stomachs in which found (to nearest whole number)
Nyctiphanes couchi	31
Mysids	26
Small teleosts	15
Crangonids	11
Polychaetes	3
Amphipods	2
Pagurids	1
Other organisms	7
Stomachs empty	33

(just over 26% of the 116 fish examined) and copepod remains were identifiable in nearly 10% of them. But, on the whole, pelagic fish caught in these months, and also in December, can be regarded as fasting. This fasting period appears to be imposed upon the fish solely by the absence of suitable food in the upper waters at this time. On or near the sea floor where food is present they do not fast, and they break their fast afterwards at any time when opportunity offers. In samples of drift-caught mackerel in early spring, most of whose stomachs are empty or contain only minute traces of food, chiefly phytoplankton, it is not unusual to find an occasional individual whose stomach is packed tightly with small pelagic fish—generally *Maurolicus pennanti*, which occur in small and localized shoals.

Bullen (1912, p. 394) is therefore correct in stating that although mackerel obtain the smaller organisms of their diet by 'filtration' the larger ones are captured by 'selective feeding'. Selective feeding has been confirmed by Damant (1921, p. 42) by direct observation in the sea. In aquarium tanks of this laboratory mackerel are fed upon fragments of squid or other suitable food which they swallow as it sinks through the water by very obvious 'visual selection'. Bullen was in error, however, in thinking (1912, p. 403) that 'when feeding upon the minor forms of the plankton mackerel are incapable of assimilating other larger prey'. The phytoplankton present in the stomachs of pelagic mackerel in early spring can have been obtained only by filtering. It is equally certain that active fishes such as *M. pennanti*, several inches in length, must have been captured by Bullen's 'selective feeding' method. There can be little doubt that mackerel obtain their food by the most profitable method depending upon the size and kind of food organisms available to them; and that, at any time of the year and wherever they may be, they fast only if there is nothing for them to feed on.

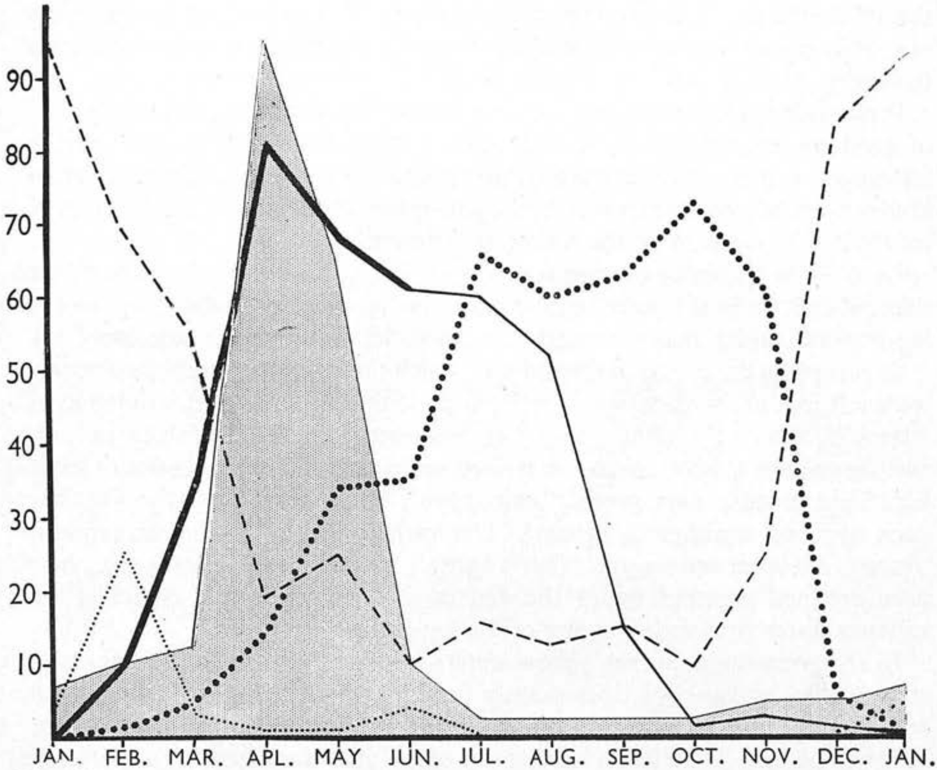
Most pelagic mackerel moving in an off-shore direction in the south-western area in the early months of the year are on migration to the spawning ground. In order to get there they leave the lower levels, where a certain amount of suitable food is available to them, for the upper layers where for a time there is practically none. The catadromous spring migration to the spawning areas is undertaken, therefore, irrespective of the presence or absence of food either at the beginning of the journey or on the way. Nevertheless, the migrating fish will at all times feed greedily if they can.

During March there is a rapid increase in the number of stomachs of pelagic mackerel containing food material—mainly copepods—and in the total quantity of food in each stomach. By the end of the month, and all through April and May, the fish feed predominantly on copepods, their stomachs being packed to bursting with these crustacea known to fisherman as 'red feed'. Although copepods predominate in the diet of the mackerel at this time a wide range of other planktonic organisms are also eaten. By about June yet another change takes place. Young pelagic stages of fish are now the mackerels' chief food, particularly *Clupea* spp., *Ammodytes* spp., and *Onos* spp. Considerable numbers of the larger crustacea also form part of the diet at this season and throughout the whole time that the fish are in shallow coastwise waters—euphausiids, mysids, the larger larvae of decapod crustacea such as *Corystes* and *Porcellana*, and even occasional pandalids, hippolytids, crangonids and similar organisms.

It will be seen (Fig. 5) that the fasting period is December—March which coincides with minimal plankton occurrence. When plankton becomes abundant the mackerel feed voraciously upon it, and continue to do so all the time that they are in off-shore waters. The change over to a predominantly fish diet, augmented with certain larger Crustacea, takes place when the mackerel have arrived back in inshore waters on their return from the spawning grounds.

Fishermen's Signs

When fishing for mackerel, especially in the Newlyn deep-sea fishery, the fishermen are influenced greatly in their choice of position for 'shooting' their nets by what are commonly known as 'fishermen's signs'. Large congregations of birds, especially diving gannets, are looked upon as good indications of the



Text-fig. 5. Diagram illustrating the changes in mackerel stomach contents in the course of one full year. The percentage of stomachs containing the chief types of food are shown thus: ......, phytoplankton; ▬, planktonic crustacea, mainly copepods; ——, non-planktonic crustacea, i.e. crangonids, pandalids, etc.; •••, fish; - - - -, empty stomachs. The contents over a whole month are recorded as for the mid-point of that month. Height of the stippled area indicates, in miles, on the same ordinate, the mean distance from land at which the mackerel examined were caught in each month.

presence of fish in worthwhile numbers. Even more reliance is placed upon the colour of the water. This has already been remarked upon by Bullen (1908, p. 287) who recognized five different kinds:

(i) Stinking water—water of a dull leaden colour having a recognizable and distinctly unpleasant smell.

(ii) Grey water—water similar in colour to the above but lacking the smell.

(iii) Blue water—very clear and transparent.

(iv) Green water—differing from blue water only in colour.

(v) Yellow water—turbid water of a distinctly yellow tint.

According to Bullen best catches of mackerel at that time (1906 and 1907) were generally, though not invariably, to be had in yellow water,[1] followed by

[1] This seems to have been first remarked upon by Pliny—quoted by D'Arcy Thompson (1947, p. 244)—who says: '*scombri quibus est in aqua sulphureus color.*'

the others in the order reverse of that given, each providing progressively poorer prospects down to the 'stinking water' in which mackerel are said never to occur.

Present-day fishermen agree that in yellow water[1] by far the best prospects of good catches are still to be had. Green water, according to their spoken testimony, comes next, but there is no unanimity of opinion about any other kinds except stinking water which, they all agree, is worst of all but fortunately is seldom encountered on the mackerel grounds.

In order to obtain more precise information on these and other points, ten selected drifters in the years 1937–1940 inclusive, were provided with special log-books in which they recorded exhaustive details of all their catches.

In recording the colour of the water in which they shot their nets the skippers were left free to use their own descriptions. For the purpose of tabulation all waters for which the term 'yellow' or 'yellowish' e.g. 'yellowish green', are used have been grouped together as 'yellow water'. All other shades of green e.g. 'light green', 'dark green', 'pale green', 'grass green' and the like have been grouped together as 'green'. The various 'blues' have been similarly treated. All other waters, e.g. 'slate', 'grey', 'paraffin oil', 'black', etc., have been grouped together under the general heading of 'other colours'. No stinking water is recorded in any of the log-books.

In the years under survey yellow waters were not very plentiful. They were encountered by log-book drifters only six times in 1937, eight times in 1938, and thirteen times in 1940. No yellow water was found by any of them in 1939.

It will be seen from Table VI that out of the total number of 27 shots made in yellow water during those four years no less than 21 (77·8%) yielded catches of over 10,000 fish, the average number per haul being 18,300.[2] Several catches of over 29,000 fish were made. In green water only 13·4% of the 918 catches consisted of more than 10,000 fish. In blue water, out of 183 catches only 1 had over 10,000 fish. The catches in other waters were poorer still.

It is quite clear from these log-book records that yellow water, when present, offers by far the best prospects of obtaining good catches. Yellow water is, unfortunately for the fishermen, not very plentiful, and in some years, as in 1939, may not occur at all.

Bullen (1908, p. 289) endeavoured by direct investigation to correlate the different kinds of water with the plankton present in it. Stinking water he found to be rich in phytoplankton and poor in zooplankton, but he was unable to offer any explanation of the reputed objectionable smell which he was himself unable to detect. He gave it as his opinion, though, that such an odour, if it did exist and could in fact be detected by fishermen, 'did not arise from the condition of plankton'. Long before Bullen's investigations, however, Pearcy (1885, p. 399), working near Shetland, had shown quite conclusively not

[1] Described by some Cornish fishermen as 'cow-dung water'.

[2] To the nearest hundred.

only that herrings avoid stinking water but that the odours were correlated with the presence of *Rhizosolenia shrubsolei* and *Thallassiosira nordenskioldii* with which the herring nets sometimes became so heavily coated that little slimy heaps of those organisms were formed on the deck as the nets were hauled in.

Supporting evidence that shoaling fish such as mackerel and herring avoid water heavily populated with phytoplankton, such as the diatom *Rhizosolenia* or the flagellate *Phaeocystis*, is provided by Russell (1915, p. 30) for mackerel, and by Savage & Hardy (1935) for herring. Although, therefore, stinking water has not been reported in the course of these investigations there appears to be no doubt that when it does occur poor fishing must be expected in it.

TABLE VI. CATCHES IN DIFFERENT TYPES OF WATER

Colour of water	Year	No. of shots	No. of shots having over 10,000 fish	Percentage of shots having over 10,000 fish	Average no. of fish per haul (to nearest hundred)
Yellow	1937	6	3		
	1938	8	5		
	1939		No yellow water		
	1940	13	13		
		27	21	77·8	18,300
Green	1937	230	42		
	1938	327	56		
	1939	247	30		
	1940	114	5		
		918	133	13·4	5,300
Blue	1937	88	0		
	1938	25	1		
	1939	31	0		
	1940	39	0		
		183	1	0·6	2,600
Other colours	1937	18	0		
	1938	38	0		
	1939	34	0		
	1940	32	0		
		122	0	0·0	2,000

In all other waters examined by him Bullen found zooplankton to be more plentiful than in stinking water, with phytoplankton also often present as well. In yellow water he found that phytoplankton was 'entirely absent' and that the zooplankton was confined almost entirely to three or four principal forms of which *Calanus finmarchicus* and *Pseudocalanus elongatus* were the most important.

Unfortunately, Bullen's data enable him to put forward only tentative explanations of the causes which give rise to the yellow colour and why, on the whole, yellow water is most likely to provide good catches. He quotes the 'somewhat conflicting opinions expressed by fishermen' to the effect that the coloration is due either to the presence of excrement arising from densely shoaling fish or to the abundant copepod 'feed' and adds that evidence provided by examination of certain plankton samples supports the latter view.

During the present investigations some of the skippers provided with log-books agreed also to work small townets and collect plankton samples from each position in which they shot their drift nets. They were all issued with exactly similar gear and given precise instructions for using it in such a way as to obtain reasonably comparable quantitative results. In spite of this the samples so obtained could not at first be relied upon from a quantitative point of view.

Nevertheless, their collection was continued and in due course many of the difficulties which vitiated their comparability were overcome so that some deductions could reasonably be drawn from them. These improvements arose in part because the skippers themselves found that, though by no means an infallible guide, their best catches of mackerel were generally obtained where the townet samples consisted of typical 'mackerel feed'—i.e. copepods in reasonable abundance—and they gradually learned to use the townets by standard methods for standard times in order to obtain comparable catches for their own information. It is therefore significant that, after the townets had been in use by selected skippers for one season, other skippers who at first would have nothing to do with them, asked, as a favour, to be issued with townets for their own use.

Examination of 300 samples retained as reliable, in association with the log-book records, support Bullen's finding that plankton catches in yellow water and light green water generally consisted almost entirely of copepods—chiefly *Pseudocalanus elongatus* and *Calanus finmarchicus*, with the former usually predominating both in numbers and in bulk. The largest samples of copepods also came from those two waters. These were preserved in formalin (5%) and having survived the war period have now been re-examined after an interval of more than ten years. In that time the preserving fluid in some of the jars containing copepods almost unmixed with other organisms such as *Limacina*, has acquired a yellow colour closely resembling that of the yellow waters on the fishing grounds. Certain yellow carotinoid substances from the copepods have gone into solution in the preservative fluid.

For some reason not understood, not all the copepod samples have liberated these yellow pigments into solution; but such samples, transferred into acetone, give the same tinge and depth of colour in a few months. There seems to be little doubt, therefore, that the underlying primary cause of the yellow coloration in the sea is the presence of copepods in concentrations so dense that their body pigments impart colour to the water. Such coloration will of course be augmented by their excreta in which the same pigments are present. Observation has also shown that the 'somewhat conflicting opinions expressed by fishermen' as quoted by Bullen (1908, p. 291) are probably not conflicting at all, and that the excrement produced by densely shoaling mackerel is also a contributory factor. Faecal matter expressed from mackerel is, in fact, generally of a yellowish or pinkish yellow colour. Mackerel, like most fish, tend to congregate in greatest numbers where their most acceptable food organisms are in greatest abundance (Herdman, 1913, p. 33). Both the fish themselves and their faecal matter will therefore be most plentiful in water already tinted by copepods and the effect of this will be to strengthen the yellow coloration.

In normal circumstances the distribution of copepods in high concentrations is characterized by its 'patchiness'; so also, in consequence, is the distribution of 'yellow water'. In years of unusual copepod abundance there will be an increase of yellow water in the form of more numerous patches, many of which will also cover greater areas. Since mackerel congregate in the yellow patches, the more numerous those patches are in any year and the greater their extent, the more favourable are the chances of their being found and fished in, with consequent benefit to the commercial fishery. In years of copepod scarcity the opposite will be true. This is in complete agreement with Allen's generalization (1909, pp. 396–97) that the catches of mackerel in May in the Newlyn deep-sea fishery are to some extent affected by the amount of sunshine in the same region during the previous February and March. This effect upon catches is an indirect and very interesting one. The phytoplankton crop depends, to some extent, upon the amount and intensity of sunlight in those early months. The abundance or scarcity of copepods is in turn partly dependent upon the magnitude of the phytoplankton crop upon which they chiefly feed. Copepod concentrations, being patchy in their distribution, cause mackerel to congregate in them, and those patches can be identified by the appearance of the water. *The effect of suitable amounts of sunshine in February and March is therefore to increase the number and size of the patches of sea in which good fishing is likely.* Obviously there must be a limit to this effect; for if, in any year, the conditions were so favourable that the greater part of the whole area consisted of yellow water rich in copepods there would be no localized concentrations of mackerel and therefore no improvement in the catches. Unfortunately, Bullen's statement with regard to zooplankton and the abundance of mackerel has for a very long time created a wrong impression. He states that 'the abundance or paucity of zooplankton during a certain number of years (1903–07) appears to be correlated with the greater or less abundance of mackerel'. It must clearly be understood that abundance of zooplankton cannot possibly increase the population of adult mackerel in the year in which it occurs. It is the 'catchability' of the mackerel already in existence that is affected and which may be reflected in the commercial catches.

SUMMARY

Of the three mackerel fisheries that formerly existed in the south-west of England, only one, the Newlyn deep-sea fishery, now remains active. The fishing grounds worked by this fishery lie in the Celtic Sea as much as 100 miles to the westward of the Scilly Islands when the season opens in March,

but the distance off becomes progressively less as the season advances until, in June, when it finishes, the participating vessels are fishing close by the land. At all times best fishing is obtained on the periphery of the areas of chief spawning intensity.

The spawning season in the Celtic Sea is a very protracted one because (*a*) the fish do not all ripen and spawn simultaneously due to (i) the divergent conditions, especially of temperature, in which different groups spend the winter, and (ii) the different lengths of the migratory journeys they must make to reach the common spawning area; (*b*) in each individual female the eggs mature in successive batches that are shed one after the other over an extended period, the duration of which is not precisely known.

In the early months of the year pelagic mackerel are often found to be fasting. This is due simply to absence of suitable food in their environment at that time. The fish will always feed when food is available.

As a general rule most mackerel are caught in patches of 'yellow' water, the colour of which is caused chiefly by localized concentrations of copepods to which the fish are attracted for feeding. Copepod abundance at the height of the fishing season must be to some extent affected—indirectly through the phytoplankton—by the amount of sunshine earlier in the season. This explains Allen's correlation between early spring sunshine and commercial catches of mackerel in late spring and early summer.

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APPENDIX I

Landings at Newlyn by Local Craft (Sail and Motor) and by Steam Drifters in the Years 1906–38 Inclusive (War Years Excepted)

	Local craft			Steam drifters		
Year	No. of landings	Total quantity in cwt.	Mean weight per landing (cwt.)	No. of landings	Total quantity in cwt.	Mean weight per landing (cwt.)
1906	2159	46265	21	1850	62551	34
1907	2190	60121	28	2962	195565	66
1908	2709	36950	15	2944	112452	38
1909	1878	27549	17	2423	112189	46
1910	1476	31757	22	2281	124122	54
1911	1581	15871	10	2156	97185	45
1912	1255	13761	11	1572	65482	42
1913	806	10419	13	1537	56176	36
1919	786	15200	19	1311	84078	64
1920	1111	16470	15	2162	112683	52
1921	1721	21932	13	1963	116931	60
1922	1824	18280	10	2185	90555	41
1923	1036	20865	20	2249	106237	47
1924	750	14613	19	2182	117540	54
1925	430	4859	11	2412	122150	51
1926	290	4441	15	1888	102390	54
1927	559	3890	7	1707	58739	34
1928	273	2924	10	1301	58827	45
1929	387	983	3	1079	43670	40
1930	173	411	2	1223	43205	35
1931	77	112	1	925	50513	55
1032	202	525	3	1014	48119	47
1933	950	2321	2	1133	51223	45
1934	988	2912	3	905	55400	69
1935	694	3002	4	856	58885	69
1936	696	4547	7	777	57177	74
1937	1131	4274	4	643	40765	63
1938	935	5134	5	641	50207	78

APPENDIX II

Differences in Temperature in February of Several European Waters in which Mackerel Live

By L. H. N. Cooper, D.Sc., F.R.I.C.

In the course of these investigations into the life history of the mackerel, the question arose whether differences in temperature of the water occurred at the time of the winter minimum between, on the one hand, the Hurd Deep, and on the other, the waters south and south-west of Ireland and near the Viking Bank west of Norway.

Hurd Deep Observations

Two lines of regular surface observations cross the Hurd Deep. These lines are worked at frequent intervals by merchant ships on shuttle service between Southampton and St Malo and between Plymouth and Guernsey. No doubt there is some uncertainty in these observations, as in all surface observations from merchant ships. Down to the level of the bottom of the English Channel vertical mixing is almost certainly thorough. We have no knowledge as to how thorough it is within the trench of the Hurd Deep.

Throughout the whole period of the Irish investigations a station was regularly worked on the Southampton—St Malo line over the eastern end of the Hurd Deep at 49° 54′ N., 2° 00′ W. Occasionally this point was omitted, but the adjacent position 50° 03′ N., 1° 55′ W. differs hardly at all in temperature and on a few occasions has been used instead.

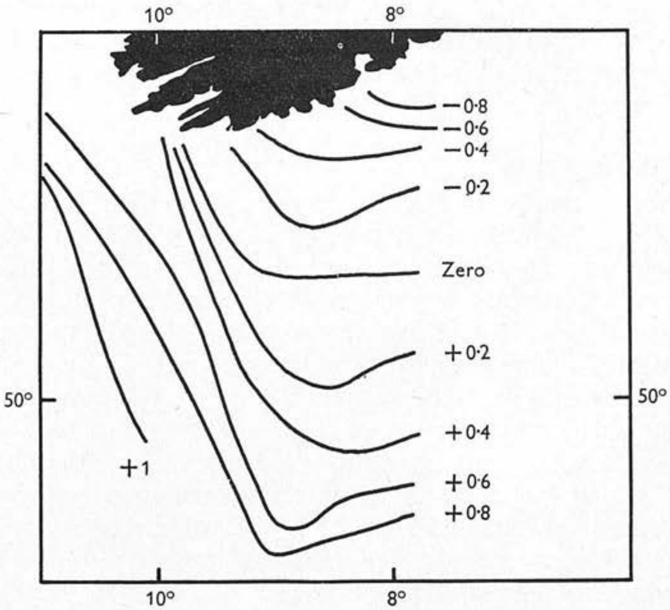
The Plymouth-Guernsey line was started in 1926 and subsequently was worked rather more frequently than the eastern line.

All data between the last January observation and 10 March have been abstracted from the *Bulletin Hydrographique* and, when necessary, graphed. The temperatures at each station about 1 and 19 February and 10 March were interpolated and the differences between the two stations evaluated. In general, the western station was the warmer, and for the eight years 1926–33, the position 49° 30′ N., 3° 02′ W. was on an average 0·4° C. warmer than the position 49° 54′ N., 2° 00′ W.

It is clear that a small temperature gradient along the length of the Hurd Deep is usual, and that the easternmost station for which most data is available lies in February over the coldest part of the trench.

Observations South of Ireland

Serial temperature observations in the Irish area have been frequently taken in February and May, but in the other winter months there are few data. The cruises were worked between 20 and 22 January in 1921 and sometime between 2 February and 10 March in the other years. In each year the mid-point in time of the Irish cruise was taken and the temperature at that time at each of the Hurd Deep positions estimated by interpolation. In the years 1926–33 the temperature of the eastern half of the Hurd Deep has been taken as the mean of these. In 1921–25, the temperatures at the easternmost position, 49° 54′ N., 2° 00′ W., have been increased by the mean correction, 0·2° C., to make them comparable with the later years.



Text-fig. 6. Differences in February temperatures between the waters south and south-west of Ireland and those at the Hurd Deep in the English Channel. Lines of equal difference—positive warmer than the Hurd Deep; negative colder than the Hurd Deep. Years 1921–33.

These Hurd Deep temperatures provide the basis line for the subsequent calculations. This temperature was subtracted from each separate Irish observation between 1921 and 1933 to give a table of differences. The mean difference at each station was then evaluated and is plotted in Text-fig. 6. Lines of equal differences were then drawn which show that the inshore water south of County Cork was colder than the Hurd Deep, and that the water south of 50° 40′ N., and west of 09° 00′ W. was warmer. The surface water above the continental slope was about 1° C. warmer.

Quite clearly the year 1929 was peculiar and so has been omitted from these calculations. Air temperatures at Scilly and Valencia were normal, whereas at Guernsey in February they were 2·7° below average. Consequently, the water over the Hurd Deep was 1·5° C. colder than the 'normal differences' for the other ten years would lead one to expect. This story concerns surface temperatures.

Bottom temperatures were also needed. The Hurd Deep surface temperatures apply to the whole water column at least down to the depth of the bottom of the English Channel adjacent to the Deep.

In the Irish area the water was almost always isothermal down to at least 120 m. Only a few stations deeper than 120 m. had been worked, namely positions *R*, *S*, *T*, *PP*, *QQ*, *RR*, and *SS* all west of 9° 55′ W., and these only in 1927, 1929 and 1932. The year 1929 has already been stated to be exceptional and it is better to use only the years 1927 and 1932 for estimating mean conditions. In these years the mean temperatures along the 150 and 200 m. contours of the shelf was about 0·9° C. higher than the temperature at the Hurd Deep. The Hurd Deep temperatures were reached at station *SS* (50° 34′ N., 11° 17′ W.) at a depth of 500 m. in 1932 and at 800 m. in 1927. In the probably exceptional year 1929, the water at the 200 m. contour was 2·5–2·8° C. warmer than at the Hurd Deep. Even at 986 m. the water was still 0·7° C. warmer.

TABLE VII

Date	Irish code letter	Position	Depth (m.)	Temp. (° C.)
10. iii. 49	*D*	50° 36′ N., 8° 04′ W.	5	9·97
		Labadie Bank	25	10·00
			60	10·00
		Sounding	*70*	—
9. iii. 49	*F*	49° 50′ N., 8° 00′ W.	5	10·30
			50	10·30
			125[1]	10·30
		Sounding	*123*	—

[1] Wire angle > 45°; true depth much less than metres of wire out.

If high temperature is a factor favouring early spawning of the mackerel, those in the Celtic Sea south of 50° 40′ N. and west of 09° 00′ W. should in most years spawn earlier than those near the Hurd Deep.

The Winter of 1949 *in Waters South of Ireland*

Steven reported (3 March 1949) that the mackerel in the area south of Ireland had started spawning several weeks earlier than normal. Since at Plymouth the winter had been remarkably mild, it seemed likely that high temperatures of the water to the westward might have been associated with the early spawning. The opportunity occurred to obtain temperatures on 9–10 March along the meridian 8° 00′ W. (Table VII).

Suitable comparable temperatures had been obtained by the Irish Fisheries Service in the years 1921–22, 1924–34 and 1938, whilst surface observations are available for other years. In 1937 water as warm was present in the area of stations *D* and *F* between mid-February and mid-March, but was evidently a short-lived intrusion into a part only of the area south of Ireland. Over the whole area for the whole of the winter, the season 1936–37 was evidently markedly colder than 1948–49. Apart from this doubtful year, it is necessary to go back to 1921 to find a similar one; even that year certainly was not warmer.

It is therefore not unreasonable tentatively to correlate the abnormally early spawning of mackerel in February and March 1949 with the notably high water temperatures.

Observations on the Western Declivity of the Norwegian Channel

During winter mackerel congregate along the western declivity of the Norwegian Channel or northern extension of the Skagerrak in the latitudes of the Orkney and Shetland Islands (p. 564). In these waters a number of hydrographic stations have been worked by the Norwegian research vessels *Johann Hjort* and *Armauer Hansen* in January or February. The suitable stations worked there in 1938 and 1939 find no counterpart in simultaneous Hurd Deep observations.

TABLE VIII

Depth (m.)	Deficiency in temperature (° C.)	
	7. i. 37	27. i. 37
100	2·4	2·1
125	2·4	2·1
150	2·5	2·0
200	2·8	2·0
250	3·3	2·0
300	3·7	2·0

TABLE IX

Depth (m.)	Deficiency in temperature (° C.) 3. ii. 37
100	2·7
125	2·4
150	2·7
200	2·8

In 1937 on 7 and 27 January, on the parallel of latitude 60° 46′ N., the temperatures of the bottom water bathing the western declivity of the Channel were lower than the Hurd Deep mean temperatures on the same date by more than 2° C. (Table VIII).

On the parallel 59° 17′ N., on 3 February 1937, the corresponding values were as shown in Table IX.

In 1937, mackerel in these waters were subjected to temperatures about 2·5° C. lower than at the Hurd Deep.

February 1930 seems to have provided an unusually small difference in temperatures, whereas January 1931 was more 'normal' (Table X). The parallel of latitude worked in both years was 60° 08′.8N.

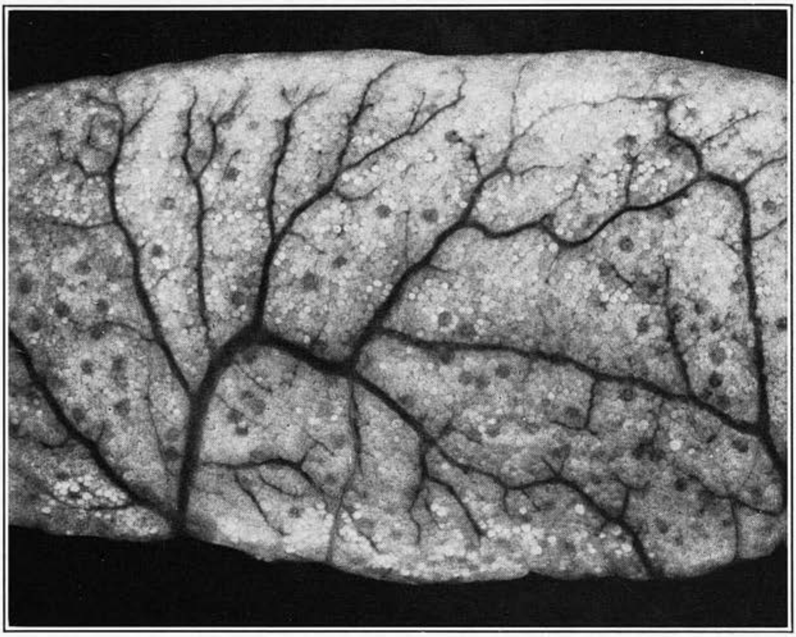


Fig. 1.

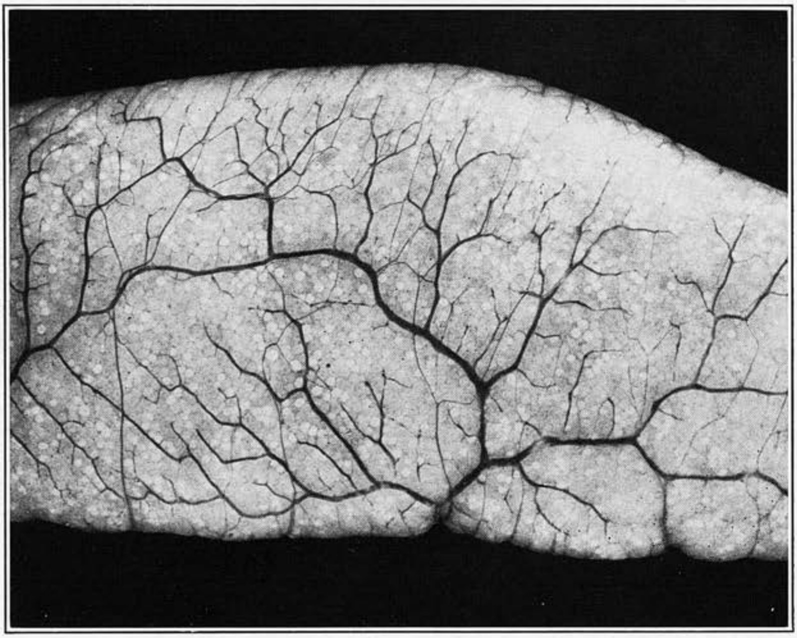


Fig. 2.

The year 1938 probably provided differences similar to 1931 and 1937.

In general we may say that the western edge of the Norwegian Channel provides temperatures 2–3° C. lower than the Hurd Deep, so that if temperature controls the time of spawning, the lag in the more northern waters should be considerable.

TABLE X

Depth (m.)	Deficiency in temperature (° C.)	
	27. ii. 30	29. i. 31
100	0·3	1·9
125	0·5	2·3
150	0·5	2·0
200	0·6	2·3

EXPLANATION OF PLATE I

Mackerel ovary in two phases. Fig. 1, the 'plum-pudding' stage, in which the widely scattered ripe eggs appear as dark spots. Fig. 2, an ovary with ripe eggs which are not visible externally but are to be found in the lumen.

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CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL, *SCOMBER SCOMBRUS* L. III. AGE AND GROWTH

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(Plate I and Text-figs. 1–4)

Introduction

The first serious attempt to determine the age and growth rate of the common mackerel (*Scomber scombrus* L.) appears to have been made by Captain Atwood in 1856 (quoted by Brown Goode, 1884, p. 116) in the Massachusetts Bay area of northern North America. Small fish caught by Atwood in October of that year measuring $6\frac{1}{2}$–7 in. in length (16·5–17·5 cm.) he believed to be the young of the year (i.e. they belonged to the O-group). Mackerel belonging to this group he calls 'spikes'. 'Blinks', 'tinkers' and 'second size' fish he assigns to the I-, II- and III-year age groups respectively, but unfortunately gives no data as to the sizes of those categories, merely stating that everyone well acquainted with mackerel makes the same groupings 'as there seems to be a line of demarkation between the different kinds which stands out prominently'. Sixteen years later, on 27 July 1872, Malm (1877, p. 409) observed large numbers of small mackerel close inshore in the Gullmarfjord near Christineberg. Several tons of those mackerel were enclosed in a seine, but only ten specimens were retained as all the others escaped through the meshes. These ten fish ranged in length from 67 to 100 mm. and Malm surmised their age to be 13 months. Collett (1880, p. 18) stated that on the coast of Norway 1-year-old mackerel are 'fingerlang'. To fish of 20 cm., taken at the end of August, he ascribed (without supporting data) an age of 2 years, with sexual maturity supervening at 3 years at an unspecified length. Marion (1889, p. 86) studied the same species of mackerel in the Mediterranean. In catches obtained at Nice between 2 and 9 May 1888 he found small individuals from 6 to 11 cm. in length, which he considered to be derived from eggs spawned during the preceding January to March, the range of size being attributed to a spread of spawning activity over those 3 months. In the Gulf of Marseilles, too, at the end of May, Marion obtained mackerel of 11 cm. which he considered to be the young of the year. At the end of the year fish of 15–18 cm. were common. Still later, at the beginning of February, both at Marseilles and farther west, Marion noted the presence of mackerel measuring 20–24 cm.

These he considered to be derived from the previous year's spawning—i.e. they were the survivors of the brood that in May, 9 months earlier, were 6–11 cm. long.

Along the shores of the Mediterranean mixed fish fry is a readily marketable commodity which commonly includes mackerel. On certain dates in 1891 Gourret (1891, p. 57) recorded the following quantities and sizes landed by a small shore fishery near Marseilles:

	kg.	cm.
17–23 April	70	4–8·5
10–13 May	30	2–3
11, 12, 14, 17 May	31	3–4
23, 26 May	6	3–5
29, 31 May	25	3–6

The April fry Gourret believed to be derived from the earliest spawning of that year, perhaps in January. The various May fry he ascribed to spawning in February (5–6 cm.); March (4–5 cm.) and even April (2–3 cm.).

In 1892 (pp. 232–3) and again in 1896 (p. 314) Cunningham expressed the belief that mackerel of from 22·2 to 23·5 cm. in length, caught on 10 June, must be more or less exactly 1 year old. Others taken on 23 June having a length range of 29·5–32·8 cm. he regarded as precisely 2 years old. Still others of 16–21 cm., taken in November, were assumed to be 16 months old. This discrepancy Cunningham attributed to individual variation in size, but was greatly perplexed by a single specimen of 13·8 cm. taken in September 'which could not have reached that length in 2 or 3 months and must have been an unusually small specimen at 14 months'. Cunningham's age estimations were based on the erroneous belief that in all the mackerel of the region spawning is 'approximately simultaneous', proceeds very rapidly when once begun, and is limited definitely to one short period of the year extending from about the beginning of June to mid-July (Cunningham, 1889, p. 25; 1896, p. 313: cf. Steven, 1949, p. 565).

Matthias Dunn (1893, pp. 4–5) expressed the firm opinion that in the western end of the English Channel young mackerel 5–6 in. long (12·7–15·2 cm.) at the end of August, are derived from that year's spring spawning. According to Dunn, these small fish stayed inshore for a further 2 months or so, growing meanwhile at the rate of about $1\frac{1}{4}$ in. (3·2 cm.) per month. By about the end of October when $7\frac{1}{2}$–$8\frac{1}{2}$ in. long (19–21·6 cm.) they disappeared from Dunn's ken until about the beginning of the following June, by which time they had attained a length of from 9 to 11 in. (22·9–27·9 cm.). Ehrenbaum (1923, p. 21) records that Knut Dahl caught 311 specimens of small mackerel ranging in length from 6 to 9 cm. in a seine net on 19 July 1905. This total was made up as follows:

Length (cm.)	6	7	8	9	(mean 7·8)
No. of fish	5	102	162	42	

Ehrenbaum considers all these fish to have been in their first year of life. Young mackerel of similar sizes have also been taken in small numbers, by other observers elsewhere from time to time without their ages having been determined or surmised. These various records are collected by Ehrenbaum (1923, pp. 12–26), who reaches the conclusion that, in general, the growth of the mackerel (*Scomber scombrus*) during the first year of life 'does not seem to amount to much over 10 cm.' (p. 22). Towards the end of their second summer Ehrenbaum considers the average length to be 20–22 cm., and 27–28 cm. in the third summer (p. 39).

Nilsson (1914, pp. 1–59) was the first investigator to make any real attempt to determine the age and growth rate of mackerel after the first year of life. Age determination in this fish is a matter of great difficulty. No bone has been found which reveals distinctive growth markings either with or without special treatment. Visible and readable markings are present on certain scales, but there is great difficulty in collecting them. They are so small as to be easily rubbed off and transferred from one fish to another in all samples collected by ordinary methods. For scales to be used reliably mackerel must be caught individually, e.g. by hook and line, and each fish kept by itself in a separate container—conditions that cannot easily be met if adequate numbers are to be dealt with. Otoliths are less clearly marked, but with practice readings can be obtained from a high proportion of them in the younger year classes—up to about 6 years. In my experience otoliths from older fish are seldom readable.

Nilsson (1914, p. 20) used scale readings checked against a few otolith determinations for age assessment of 208 specimens. From this somewhat scanty material he gives the following lengths reached by mackerel at the end of each year of growth up to and including 6-year-old fish (lengths measured to tip of tail):

End of 1 year	Maximum recorded length 22·9 cm.
„ 2 years	23·5–30·6 cm.
„ 3 years	31·1–33·9 cm.
„ 4 years	34·4–36·1 cm.
„ 5 years	36·7–38·5 cm.
„ 6 years	39·1–40·3 cm.
„ 7 years	40·9–?

Nilsson's findings are in agreement, therefore, with those who ascribe to the mackerel a growth of 20 cm. or more in the first year of life, as against those who consider fish of this size to be at or near the end of their second year of life.

This divergence of opinion as to the growth rate of the mackerel, at any rate in its early years, has persisted. As late as 1939 Le Gall (p. 14) gives the following figures based on length frequencies (not given) and the distribution throughout the year of mackerel shoals comprising fish of different sizes.

End of 1 year		8–11 cm.
,,	2 years	18–21 cm.
,,	3 years	26–28 cm.
,,	4 years	30–32 cm.
,,	5 years	35 cm.

At the same time, Steven and Corbin (1939, p. 18) made considerably different tentative assessments of age and growth rate based on scale and otolith readings. These were:

End of 1 year			?
,,	2 years	Up to	27 cm.
,,	3 years	,,	31·5 cm.
,,	4 years	,,	33·5 cm.
,,	5 years	,,	35·0 cm.
,,	6 years	,,	35·5 cm.
,,	7 years	,,	36·0 cm.

According to Sette (1943, p. 154), on the American side of the North Atlantic the fry of the common mackerel reach a length of about 50 mm. in about 70 days after hatching—i.e. by about the end of July for the majority of them. Subsequently, Sette (1950, p. 312) states, without supporting data, that these July fingerlings reach a length of 8 in. (i.e. just over 20 cm.) by September; and that they range, in their second year of life, from 25 cm. in early summer to 32 cm. by fall.

Recently, Le Gall (1950) has repeated his 1938 figures concerning age and growth of mackerel, again without supporting data, but with the accompanying remark that 'la présence, en quantités parfois très abondantes de la mi-Juin à la fin de Septembre, de jeunes maqueraux de 7 à 11 centimètres, confirment l'opinion que nous avons deja émise sur la croissance de ce poisson'.

The two schools of thought on mackerel growth are at variance mainly in their conclusions concerning rate of growth in the first year of life, one school placing the first year's increment at 10 cm., or a little over, while the second attributes a length of 20 cm. or more at the end of the first year. Ehrenbaum, of the first school, supports his view by saying that the mackerel is hardly likely to grow faster than cod and haddock, which at the end of their first summer measure only about 14 cm. (1923, p. 23).

Striking confirmation of rapid growth by mackerel in their first year of life has recently been provided by Dannevig (1947, p. 93; 1948, p. 219), who has been able to make direct observations on the growth of young mackerel in his fish-hatchery basins at Flødevigen, Norway. On 6 August 1939, a number of young mackerel, 8 cm. in length, appeared in the leads between the basins and the lobster hatchery. One was caught and placed in an aquarium where there were large quantities of small Crustacea, and throve remarkably. Later it could be provided with only dead food which did not agree with it, and it died on 1 September being then 10·5 cm. long. The fish had grown 2·5 cm. in 25 days. Later, on 14 September, about twenty small mackerel were observed in the oyster basins. Their lengths were approximately 15 cm. The basins had been emptied in the spring and those small mackerel must have entered as eggs contained in the water pumped into the basin in May–June of the same year. Dannevig states that young fish could not have passed through the centrifugal pump and lived. He is therefore in no doubt that those mackerel were young fish of the current year and that they had reached a length of 15 cm. in about 4 months. This agrees closely with Dunn's figures of 12·7–15·2 cm. length at the end of August in the English Channel. There can be now no doubt that mackerel may reach a length of 20 cm. or more in the course of their first year of life.

Methods

Investigations by the present author into the life history and biology of mackerel in the English Channel and Celtic Sea have included researches into ages and growth rates. Otoliths have been collected from a total of 8422 fishes, of which 6261 (74·3 %) have been readable and 2161 (25·7 %), mainly in the higher length groups, have been unreadable. In addition, scales from 1364 fish were collected, but scale reading was discontinued when it was found that a sufficient proportion of otoliths could be read to give reasonably satisfactory results.

The otoliths were collected from each fish by cutting transversely through the head behind the eye at a point immediately in front of the small cavities in which the otoliths lie. There are two otoliths on each side, but the smaller one is useless for age determination. After the cut is made the brain is removed from the remaining posterior part of the cranium. The large otoliths can then be removed, one at a time, by probing for them with a weakly-sprung sharp-pointed forceps. At first this may present some difficulty, but with a little practice the operation becomes both simple and speedy.

As thus obtained, each otolith is covered with soft tissues that must be completely removed before drying. This cannot conveniently be done immediately, as too much time would be taken up in disposing of the sample of fish. The otoliths are therefore stored under water until they can be cleaned. This is best done by making shallow holes in a block of hard, close-grained wood about 9 in. square. One hundred such holes, preferably $\frac{5}{8}$ in. in diameter and $\frac{3}{16}$ in. deep, can conveniently be made in such a block. They should be arranged in regular rows of 10×10. Above the uppermost hole in each vertical row the numerals 1–10 are clearly marked. The whole upper surface of the block, including the shallow holes, should then be painted black with a waterproof paint that will retain the water with which the holes have to be filled. A specially made block of black plastic material would be even more suitable. On removal from the fish the otoliths are placed in the appropriate hole which is filled with water to keep them wet.

As soon as possible after the sample has been dealt with the otoliths must be divested of all soft tissues adhering to them and placed in numbered containers. Envelopes are unsuitable as the otoliths are so small and brittle that they become lodged in the corners, are hard to see, and often get broken. The best method is to glue small cardboard pillboxes by their bottoms on a square piece of cardboard—100 boxes arranged in rows of 10×10 to each piece of board.

To clean the otoliths two pieces of cane about 3 mm. in diameter and 15 cm. long are used. Before use each piece is sharply pointed at one end and the points worked gently backwards and forwards on a piece of glass. This breaks up the single fine point and releases the fibres so that a tiny brush of just the right stiffness is formed. With two brushes thus prepared the otoliths can be easily and completely cleaned in water in a solid watch-glass, preferably of black glass, under the low power of a dissecting microscope.

Mackerel scales are very small and easily rubbed off. Special precautions had therefore to be taken to ensure that the scales removed from a fish really belonged to it. Nilsson's method of using hooked fish for scale-reading purposes was therefore adopted. Each fish, on removal from the water carefully suspended from its hook so as not to touch anything, was lowered tail first into a clean, grease-proof paper bag. Both bag and fish were then held firmly in the left hand while the hook was removed. By adopting this method, very few scales actually became dislodged from the fish, and any that were rubbed off were inside that fish's own bag.

For age determination, scales from the anterior part of the body just below and slightly behind the pectoral fin have invariably been used. A scraping in this position is made with a scalpel and the small mass of scales so collected is washed off into a small specimen tube ($1\frac{1}{2} \times \frac{1}{2}$ in.) almost filled with clean water. The tube is then corked. Groups of 100 tubes are used, fitted into a 10×10 arrangement of holes in a block of wood, the holes smaller and deeper than those made for the reception of otoliths.

The scales are collected and stored in tubes because they are too small to be removed individually with a pair of forceps, followed by dipping in water, cleaning between the thumb and first finger of the left hand, and mounting on a microscope slide—as can be done with herring and pilchard scales, for example. In their tubes they can be left for an indefinite period before eventual cleaning and mounting. If left for more than a few days the contents of the tube will smell strongly, but this does no harm; indeed it is an advantage because the scales are more easily cleaned after the organic matter covering them has decomposed. In a normal scraping anything up to 500 scales may be present. From amongst these at least three scales should be selected for mounting. In most samples, scales of many shapes and sizes will be found of which only a few will be readable. Most kinds are well illustrated by Nilsson (1914, plate I, figs. 1–13). The clearest and most consistent zoning and ringing are found on those shaped as in Nilsson's figs. 8 and 11. At least three scales of this type should be looked for amongst the mass of others, and removed to a second watch-glass. There they must be cleaned, in water, under a binocular dissecting microscope, using brushes made from pieces of cane in the way described above. Three such scales are shown in Pl. I, figs. 1–3.

Age and Growth

In this investigation scales from each of 1364 fish were mounted on microscope slides previously smeared very lightly with prepared egg albumen. All these scales were separately 'read', and it was found that in 1343 out of the 1364 fish (98·5 %) the readings of all three scales were in agreement. In the remainder, the three scale readings did not all agree. This degree of discordance is not excessive and gives good grounds for assuming that the readings are reliable. Even more confidence can be placed in them when comparison is made with otolith readings from the same fishes. Omitting those fishes that gave discordant scale readings, it is found that in only fifteen out of a total of 1343 individuals (1·1 %) did the scale readings differ from those of the otoliths. Difficulty in reading the otoliths can very easily account for this discrepancy. These results are shown in detail in Table I.

In consequence of this satisfactory agreement between scale and otolith readings, the collection of scales was discontinued and only otoliths were taken from later samples. In this connexion it must be emphasized that a high proportion of otoliths were rejected as unreadable. Included in this group are all otoliths whose readings were to any appreciable extent doubtful. It is believed to be better to reject completely a doubtful reading than to include it in any group to which it 'probably' belongs.

In the mackerel there are two otoliths on each side—a larger and a smaller one. The latter, flat and somewhat irregularly crescent-shaped in outline, is generally almost completely transparent and never exhibits readable 'ringing' and 'zoning' (Nilsson, 1914, plate I, fig. 16). The larger otolith is thickest and widest at its posterior end, tapering towards its anterior end where it terminates in two points of unequal length. Nilsson (p. 23) states that this otolith 'can at times have fairly distinct annual rings, especially on the longer of the two points'. In the present investigations reliable readings have been more easily obtained at the blunt posterior end of the otolith.[1] While it is true that

[1] In Nilsson's own figures (plate I) the markings are clearest at the blunt ends of the otoliths shown.

markings are often most distinct on the longer point, secondary markings are often so much in evidence that interpretation is difficult or impossible.

Reading is best carried out in a solid watch-glass made of jet-black glass. The otoliths are viewed under water or alcohol by direct illumination.[1] Thus examined, the central part of the otolith shows up as opaque chalky white. In fish of more than 1 year the dense central portion is surrounded by a dark, narrow 'ring'. With increasing age further zones and rings are formed (see Pl. I, figs. 4–6).

TABLE I

Serial no. of sample	Total fish	No. of fish with discordant scale readings	All scales in agreement but differing from otoliths	Percentage of fish with all scales and otoliths in agreement
13A	100	6	1	93
15	61	4	1	92
24	96	0	0	100
29	93	0	0	100
31	71	0	5	93
32	99	0	0	100
37	13	0	2	85
39	49	0	0	100
41	100	10	1	89
44	20	0	0	100
45	40	0	0	100
46	50	0	0	100
47	41	0	0	100
48	39	0	0	100
49	51	0	0	100
50	40	0	0	100
52	58	0	1	98
54	45	0	0	100
55	48	0	2	96
56	50	0	0	100
57	100	0	2	98
58	100	1	0	99
Total	1364	21	15	97·4

The central zone is first laid down. This is followed by the first ring which, although formed in winter, does not generally become clearly defined until late spring or early summer when the new season's zone, now forming outside it, serves to show it up. This applies also to all the dark transparent winter rings that are laid down in subsequent years.

Unlike a ring, a zone is recognizable while growing, long before the next ring is laid down demarking its final limit. Thus a 2-zoned fish is one in which a fully developed central zone is surrounded by a fully formed ring, and a second zone, the latter being either partly formed or completed.

New zones, narrow and obviously of recent origin, begin to show up in late spring and early summer. Thus a fish in its second year, caught say in September, will have a distinct second zone clearly noticeable. Its otolith reading will therefore be '2 zones 1 ring', recorded as '2–1'. The same fish

[1] Otoliths that have been stored dry for a long time float in water; alcohol must then be used.

will continue to have a reading of '2–1' until next May or June when a third zone, newly forming, will show up the second winter ring. Readings of '1–1', '2–2', '3–3' have therefore seldom been made; for by the time that the new zone has shown up the immediately preceding winter ring clearly, it has become itself recognizable and must be recorded. It will be convenient, therefore, to discuss otolith readings in terms of zone numbers. An otolith with two zones will obviously have a winter ring between them; a three-zoned otolith will have two intervening rings; and so on.

Since new growth begins about May and continues rapidly throughout the summer and autumn, distinction must be made between fish caught at or near the beginning of the growing season and those caught at or near the end of it. In the early part of the year, before the new seasons's growth has got well under way, a fish whose otoliths record two zones will have completed 2 full years' growth, and really should read '2 zones–2 rings'. By the time the second ring becomes definitely recognizable, the third zone will also be showing up and that fish becomes '3–2'. In late summer and autumn, a fish recording two zones is really aged only 1+; i.e. the second full year's growth is not completed: similarly a three-zoned fish will be 2+, and so on.

Otoliths from a total of 8422 fish, obtained over the years 1936–40 and 1948, have been examined. Of these, readings have been possible from 6261 fish, and 2161 (25·7 %), mainly from individuals over 6 years of age, have been unreadable.

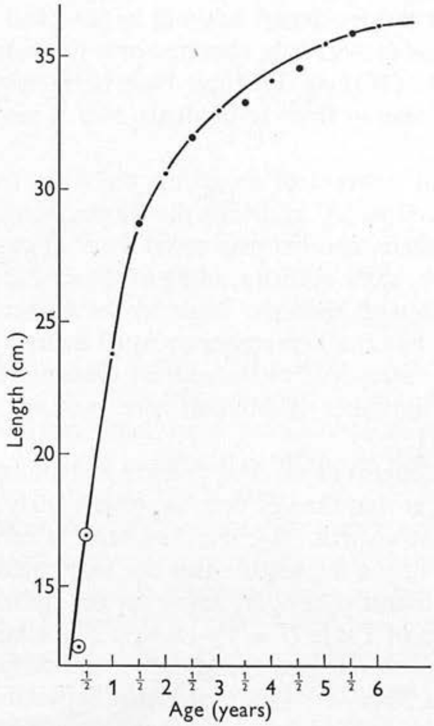
It has been found convenient to group the 6261 fish that gave otolith readings into two groups, 'A' and 'B', the former having 1 September and the latter 1 May as their 'approximate mean date' of capture. Fish included in group A, having the same otolith reading as those of group B, will therefore have a lesser mean length than the latter by the amount of growth that has taken place in the 8 months September to April inclusive.

The mean lengths measured to the nearest centimetre below and suitably corrected, obtained for fishes of different zone readings grouped in this way are given in Table II.

In Text-fig. 1 the lengths of the May fish are plotted against the numbers of otolith zones which, at that time of year, represent fairly exactly the numbers of completed years of growth. A curve has been fitted empirically to those points. The lengths of the September fish can be plotted on the same graph. On inspection it is found that if, in doing so, the number of years' growth recorded in column 2 of Table II as 1+, 2+, ..., be taken to read $1\frac{1}{2}$, $2\frac{1}{2}$, ..., then the points (large on the graph) conform remarkably closely to the curve already drawn for the May fish. This means that September fish with (n) zones on their otoliths have completed ($n-\frac{1}{2}$) annual increments of growth; that is to say, that half the total growth increment for the year is completed during the 4 months of May–August inclusive, while the other half is spread over the months September–April inclusive.

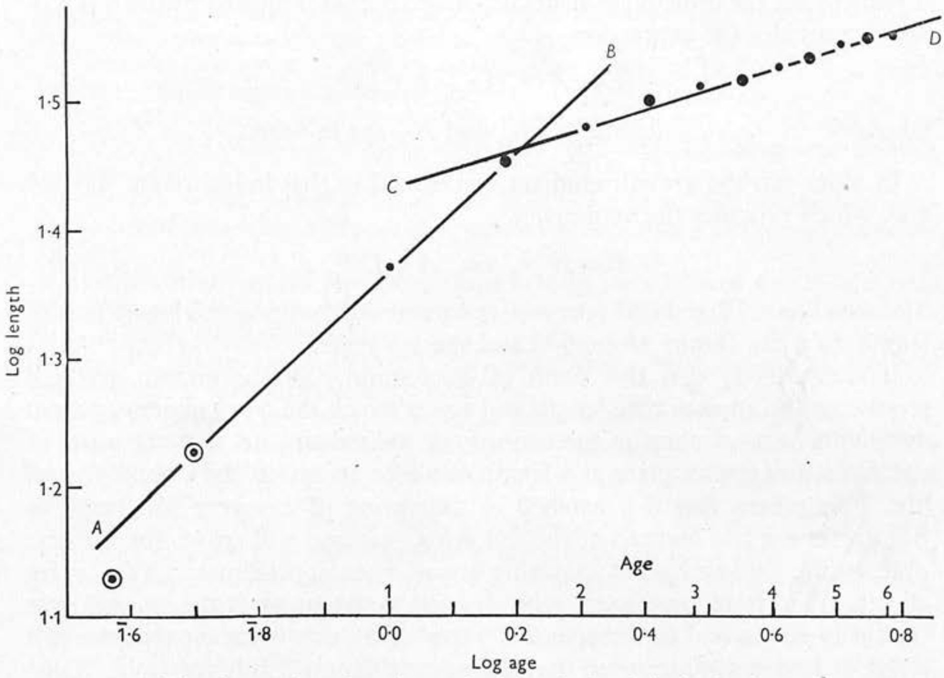
TABLE II. MEAN LENGTHS OF FISH OF DIFFERENT ZONE READINGS (UP TO 6) IN SEPTEMBER AND MAY

	Mean date, *c.* 1 September		Mean date, *c.* 1 May	
No. of zones on otoliths	No. of years' growth	Mean length	No. of years' growth	Mean length
1	< 1	—	No records	
	—	—	1	23·8
2	1 +	28·7	—	—
	—	—	2	30·6
3	2 +	32·1	—	—
	—	—	3	33·0
4	3 +	33·3	—	—
	—	—	4	34·1
5	4 +	34·6	—	—
	—	—	5	35·5
6	5 +	35·9	—	—
	—	—	6	36·2



Text-fig. 1. Growth of mackerel up to 6 years.

Small mackerel of less than 15 cm. in length are seldom caught in this area. Occasionally, however, they put in an appearance in shallow water (Steven, 1948, p. 536). Ford (unpublished data) obtained a few small mackerel in Plymouth Sound in August 1926 having a mean length of 15·3 cm.; and again in August 1927 he caught about fifty similar fish in a sprat seine having a mean length of 13·6 cm. (range 12·5–15·2 cm.). In 1937 very large numbers of small mackerel appeared in and around Newlyn harbour, in Cornwall, and in the first days of August the present writer caught 273 of them having a mean length of 12·7 cm. (range 8·0–16·4 cm.). At the end of the same month



Text-fig. 2. Length and age of mackerel—logarithmic plotting.

84 more small fish were taken having a mean length of 16·9 cm. (range 14·0–17·9 cm.). Assuming that half a full year's growth takes place, on the average, in May–August inclusive, the fish caught in the first week of August 1937 may be assumed to have made about three-eighths of a full year's growth. The small fish taken at the end of the month would have completed approximately half a year's growth. These points are also plotted (in circles) on the graph in Text-fig. 1 and appear to conform to the curve derived from plotting the age-length relationships of older fish.

In Text-fig. 2 the same age-length data are plotted on a double logarithmic scale. When this is done it is found that for fish of 2 years and upwards the points fall on or near the straight line *CD* and that those appertaining to younger fish fall on or near another straight line AB, with the exception of the early August fish which do not quite conform. On the assumption that they have grown about three-eighths of their full year's increment, the mean length of these fish should have been 14·6 cm. to fall on the line AB, a figure that lies well within the length range of the 273 fish from which the mean was derived and may be accepted as being in reasonable agreement for all practical purposes. On the other hand, an adjustment of 3 weeks in their assumed age is all that is necessary to obtain agreement.

There can be little doubt therefore that in the young fish up to about 2 years of age the growth gradient conformed to that indicated by the line AB, which provides the expression

$$L \propto A^{0\cdot49}, \text{ i.e. } A \propto L^{2\cdot06},$$

where L = length in cm., and A = age in years.

In older fish the growth gradient conformed to that indicated by the line CD, which provides the expression

$$L \propto A^{0\cdot15}, \text{ i.e. } A \propto L^{6\cdot65}.$$

The two lines AB and CD intersect at a point representing the logarithms of length 29·3 cm. (limits 28·6–29·5) and age 1·6 years.

It seems likely that this point of discontinuity in the growth gradient represents the approximate length and age at which the onset of active sexual development takes place in the majority of individuals, i.e. that the onset of sexual maturity takes place at a length of about 29 cm. in the second year of life. This means that fish hatched in the spring of any year will begin to 'fill up' in the late autumn of the following year and will spawn for the first time during the subsequent spawning season when approximately 2 full years of age. This is in agreement with Nilsson's statement (1914, p. 41) that 'maturity is reached at the age of 2 years' if by this is meant that the fish arrive at first spawning when they are approximately 2 full years old. Confirmation of these results has been obtained from simultaneous observations on gonad development. Le Gall (1950, p. 71) also states that the onset of first maturity takes place at or over a length of 26–28 cm., but ascribes an age of 3 years to such fish.

Onset of Sexual Maturity

Data bearing on the onset of sexual maturity in the mackerel of this region have been obtained by examination of 9334 fish in which sex and gonad condition have been determined. The determinations were made by naked-eye observation. Young individuals in which the sex could not be decided by this means have been recorded as immature fish. The later stages of development of the sexual organs have been classified according to a scheme similar to that used internationally for the herring and other clupeoids (see Jensen, 1950, p. 6), but suitably modified for the somewhat special characteristics exhibited by the mackerel.

Stage O. Immature juveniles. Sex not ascertainable by naked-eye examination.

Stage I. Virgin individuals. Sexual organs very small but sex ascertainable by naked eye. Ovaries rich wine colour and very slender torpedo shape; individual eggs indistinguishable. Testes much paler in colour than the ovaries; also thinner and more blade-like.

Stage II. Maturing virgins (maiden fish) and recovering spents. In virgin fish the ovaries are slightly larger now than in stage I and individual eggs begin to be distinguishable. Testes also enlarging; paler in colour than ovaries. In recovering spents, at this stage, both ovaries and testes are also quite small but flabbier than in virgin fish and generally somewhat bloodshot.

Stage III. Sexual organs considerably larger and occupying about half of the ventral cavity. Differences between virgin fish and recovering spents now scarcely distinguishable.

Stage IV. Sexual organs still growing. Ovaries becoming a pronounced orange-yellow colour with conspicuous opaque eggs. Testes becoming a clear creamy or milky colour.

Stage V. Sexual organs now filling ventral cavity. In the ovary superficial blood-vessels have become large and conspicuous. No transparent eggs. Testes assuming a fairly uniform milky whiteness.

Stage VI. *Testes*—large, firm and clean milky white. Small amount of ripe milt can be expelled from them on slight pressure.

Ovaries. In the female stage VI has been subdivided into two stages:

Stage (♀) VI A. Ripe translucent eggs scattered throughout unripe eggs giving rise to a 'plum pudding' appearance (see Steven, 1949, p. 565 and plate I). No ripe eggs free in the lumen.

Stage (♀) VI B. Ripe eggs present in the lumen of the ovary which generally must be opened to find them. Externally, the ovary may appear to be in stage V or VI A, but the presence of ripe eggs free in the lumen indicates that one or more batches of eggs have already been spawned. After several batches have been shed the ovary becomes progressively more flabby and bloodshot, especially posteriorly.

Stage VII. *Spent fish*. Ovaries slack with only residual eggs. Very bloodshot. Testes also small, flabby and bloodshot.

A stage VIII as used for herring (Jensen, 1950, p. 6) has not been separately distinguished.

The 9334 fish examined for sex comprised 995 immature juveniles whose sex was not evident from naked-eye observation. The remainder comprised 4031 males and 4308 females. Of these 803 males and 681 females were in maturity stage I—i.e. were virgin fish in which signs of rapid gonad development towards ripening are still absent though the sex is determinable by naked-eye observation. Some females whose lengths ranged from 22 to 28 cm. had ovaries of quite small size that nevertheless exhibited a typically shotten appearance, but which, after the most careful examination, always failed to reveal any residual ripe eggs in the lumen. The explanation appears to be that, in those fish, the gonads had progressed a considerable way towards ripeness and then assumed a spent appearance without any ripe eggs having been actually produced and shed. Similar precocity was detectable also in some males over a length range of 24–28 cm. Since these fish—designated 'false stage VII'—had not spawned, they have been grouped with stages O and I as maiden fish which had not yet reached first maturity.

In Table III the total numbers of fish at the various stages of gonad development have been entered against the length in cm. From this table it will be seen that all fish under 18 cm. in total length were in those stages of immaturity in which the sex was not determinable by naked-eye examination. Fishes in this stage were not uncommon up to a length of 22 cm. after which their numbers diminished and they were almost totally absent in all sizes exceeding 29 cm. Fishes in stage I begin to appear in small numbers at lengths of from 18 to 20 cm. and remain common up to lengths of just over 30 cm. Fishes at stage II, which includes maiden fish with gonads in the very early stages of active ripening, and recovering spents in which the gonads have gone far towards resuming their original appearance in maiden fish, begin to appear at 21 cm. and become plentiful at lengths of 27 cm. and upwards. The later stages, up to and including stage VI, do not appear in any numbers until lengths of 30 cm. and upwards are reached. The table further reveals that spent fish may be at times noticeable in the catches at smaller sizes than fully ripe fish. There are probably two explanations for such apparently anomalous occurrences: (i) that fish in a state of precocious maturity and giving a false appearance of 'spentness' have been mistaken for true spents; and (ii) that, by some vagaries of the fisheries or of sampling, spent fish on occasion were obtained for examination from schools of smallish fish from which no samples were collected when they were in the spawning state.

In further reference to Table III it will be seen that the immature fish of stages O and I and precocious stage VII are chiefly confined to fish of less than 29 cm. in total length—i.e. they are grouped on the left of the line *AB* drawn through the table—and that stages III–VII are comprised mainly of fish of 30 cm. and upwards, i.e. they are grouped on the right of the line *AB*. Stage II may be regarded as a transition phase in which the ripening process is actively beginning but has not yet reached the state of very rapid gonad development associated with stage III onwards.

This grouping of the fish in Table III on either side of a line falling between lengths of 29 cm. and 30 cm. agrees well with the figure of 29·3 cm. as the point of discontinuity in the curve of growth derived from plotting log length against log age. There can be little doubt, therefore, that the change in the growth gradient in respect of the age-length relationship is very closely associated with the onset of first sexual maturity. This is further borne out by the fact that if the percentage of fish exhibiting gonad stages II–VII inclusive (Table III) is plotted against length, the derived sigmoid curve

TABLE III. LENGTH DISTRIBUTION OF THE VARIOUS REPRODUCTIVE STAGES

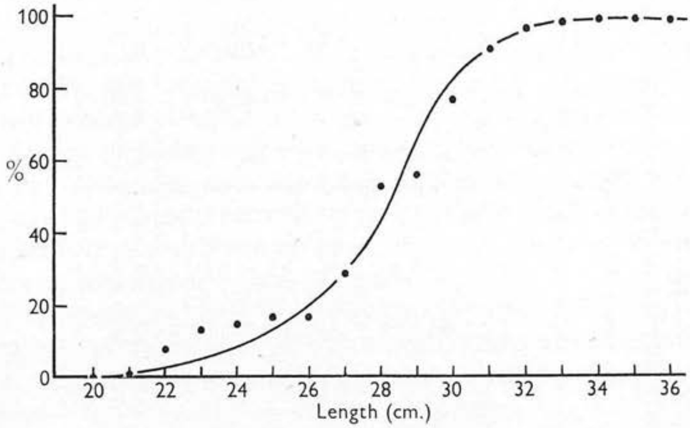
Length of fish (in cm.)

State of sexual organs		< 18	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	Totals
O:		339	75	88	98	120	122	62	19	19	18	13	9	9	2	1	1	—	—	—	—	—	—	—	—	—	995
I:	♂♂	—	1	1	3	14	37	52	40	31	67	97	124	179	98	38	15	5	1	—	—	—	—	—	—	—	803
	♀♀	—	*1*	*14*	—	*42*	*87*	*63*	*20*	*46*	*92*	*99*	*99*	*72*	*27*	*9*	*7*	*2*	*1*	—	—	—	—	—	—	—	*681*
False VII:	♂♂	—	—	—	—	—	—	—	2	3	14	20	9	—	—	—	—	—	—	—	—	—	—	—	—	—	48
	♀♀	—	—	—	—	—	*1*	*2*	*2*	*1*	*2*	*12*	*8*	—	—	—	—	—	—	—	—	—	—	—	—	—	*28*
II:	♂♂	—	—	—	—	1	1	1	—	2	5	9	23	38	51	61	52	34	29	20	10	11	2	2	1	—	353
	♀♀	—	—	—	—	*2*	*21*	*27*	*15*	*17*	*28*	*58*	*145*	*174*	*129*	*64*	*41*	*35*	*35*	*23*	*17*	*7*	*5*	*2*	*1*	—	*846*
III:	♂♂	—	—	—	—	—	—	—	—	—	—	1	—	1	5	7	31	26	25	13	22	5	4	—	—	—	140
	♀♀	—	—	—	—	—	—	—	—	—	—	—	*2*	*4*	*10*	*20*	*52*	*89*	*101*	*101*	*60*	*48*	*11*	*5*	*3*	*1*	*507*
IV:	♂♂	—	—	—	—	—	—	—	—	—	—	—	—	2	5	6	20	29	44	46	39	24	6	13	—	—	234
	♀♀	—	—	—	—	—	—	—	—	*1*	—	—	—	—	*2*	*11*	*38*	*33*	*59*	*69*	*82*	*64*	*34*	*8*	*1*	*1*	*403*
V:	♂♂	—	—	—	—	—	—	—	—	1	—	—	—	2	6	12	34	78	85	87	83	46	12	4	4	1	455
	♀♀	—	—	—	—	—	—	—	—	—	—	—	—	—	*5*	*12*	*43*	*60*	*71*	*82*	*62*	*40*	*25*	*10*	*4*	—	*414*
VI:	♂♂	—	—	—	—	—	—	—	—	—	—	2	1	7	61	106	169	231	191	186	149	69	36	13	—	1	1222
VI A:	♀♀	—	—	—	—	—	—	—	—	—	—	—	—	—	*4*	*10*	*19*	*27*	*42*	*29*	*20*	*15*	*7*	*2*	—	—	*175*
VI B:	♀♀	—	—	—	—	—	—	—	—	—	—	—	—	*2*	*13*	*35*	*72*	*88*	*87*	*70*	*46*	*34*	*23*	*5*	*3*	*2*	*480*
VII:	♂♂	—	—	—	—	—	—	—	—	1	6	17	61	53	64	96	101	131	96	78	46	19	5	1	1	—	776
	♀♀	—	—	—	—	—	—	—	—	*1*	*1*	*10*	*50*	*79*	*80*	*72*	*83*	*95*	*107*	*82*	*68*	*29*	*14*	*2*	*1*	—	*774*
Total fish		339	77	103	101	179	269	207	98	123	233	338	531	622	562	560	778	963	974	886	704	411	184	67	19	6	9334
Total: O, I, False VII		339	77	103	101	176	247	179	83	100	193	241	249	260	127	48	23	7	2	—	—	—	—	—	—	—	
Total II–VII		—	—	—	—	3	22	28	15	23	40	97	282	362	435	512	755	956	972	886	704	411	184	67	19	6	
Percentage II–VII in total fish		*0·0*	*0·0*	*0·0*	*0·0*	*1·68*	*8·18*	*13·53*	*15·31*	*18·69*	*18·45*	*28·70*	*53·11*	*58·20*	*77·40*	*91·43*	*97·04*	*99·27*	*99·79*	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	*100·0*	

has its point of inflexion at a length of 28·8 cm. (limits 28·4–29·2) (Text-fig. 3).

Weight-Length Relationship

Weights to the nearest gram of a number of fish covering the whole range of available lengths have been determined. For this purpose fish under 20 cm. in length are arranged in ½ cm. size-groups, measured to the nearest ½ cm. below. Fish over 20 cm. are placed in 1 cm. size-groups, measured to the nearest cm. below. A correction of half a group unit has been added to all mean lengths. The weight-length data so obtained are shown in Table IV. When plotted logarithmically (Text-fig. 4) a definite discontinuity is manifest in the weight-length relationship at 27·9 cm. mean length (with rather wide limits of *c.* 25·7–31·6) and 135 g. mean weight.

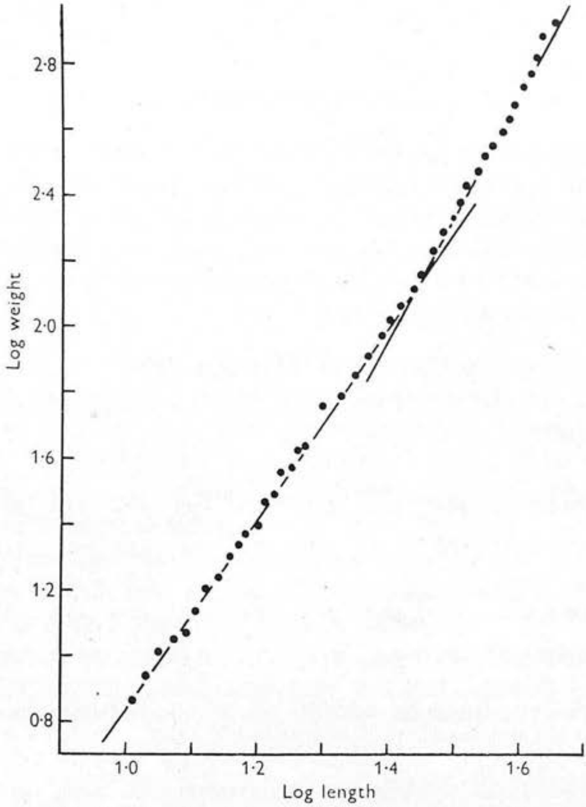


Text-fig. 3. Percentage of all fish examined showing gonad stages II–VII inclusive: in centimetre length-groups.

From 28 cm. down to 10 cm. (the smallest fish weighed) the weight-length relationship is expressed by $W \propto L^{2\cdot 86}$. From 28 cm. upwards the weight increases much more rapidly in relation to length and conforms to the expression $W \propto L^{3\cdot 54}$. This applies only to fish in the early part of the year when they have recovered from the spent condition and are again actively ripening; comparative figures for newly spent fish have not been obtained.

A change in the weight-length relationship of growing fish appears to manifest itself at a slightly earlier stage than the change in the length-age relationship, but the difference is doubtfully significant, and anyhow the two critical mean lengths are sufficiently close to suggest that both changes may be initiated simultaneously at the onset of first sexual maturity.

Age determination by direct methods has not been possible beyond 6 years. Further researches and improved techniques may increase the range of direct readings—from otoliths, scales or other body structures—by a few years;



Text-fig. 4. Weight-length relationship of mackerel: logarithmic plotting.

TABLE IV. WEIGHT-LENGTH RELATIONSHIP

Length group (cm.)	No. of fish	Mean weight (g.)	Length group (cm.)	No. of fish	Mean weight (g.)	σ
10·25	7	7	21·5	11	62	4·7
10·75	10	9	22·5	17	72	6·8
11·25	22	10	23·5	25	81	7·8
11·75	21	11	24·5	33	95	8·0
12·25	32	12	25·5	26	105	12·9
12·75	32	14	26·5	18	115	8·6
13·25	38	16	27·5	26	129	9·3
13·75	25	17	28·5	39	146	17·0
14·25	26	20	29·5	49	169	12·0
14·75	32	22	30·5	49	194	14·3
15·25	20	24	31·5	54	217	16·2
15·75	10	25	32·5	60	241	17·7
16·25	14	30	33·5	72	271	23·6
16·75	12	31	34·5	96	300	25·0
17·25	2	37	35·5	77	331	31·7
17·75	5	37	36·5	100	354	35·9
18·25	1	42	37·5	88	392	44·5
18·75	3	43	38·5	67	430	47·0
19·25	—	—	39·5	43	481	34·4
19·75	—	—	40·5	24	542	55·8
20·5	6	58	41·5	8	584	29·1
			42·5	6	669	24·3
			43·4*	3	782	—
			46·1†	1	851	—

Specimens up to 20 cm. in length were weighed all together in their length groups and the mean obtained by a single calculation: σ was therefore not obtained.

* Actual mean (without correction) of fish measured to nearest mm.

† Actual measurement to nearest mm.

but such determinations are unlikely in the foreseeable future to cover the entire life span. It is worth while, therefore, to use the data already available to calculate approximate theoretical mean lengths and mean weights attained by fish in each year of life until a length of 43 cm. is reached—this being the maximum length recorded in this investigation, except for a single fish of 46·1 cm. total length weighing 851 g.

TABLE V. LENGTH AND WEIGHT OF MACKEREL AT DIFFERENT AGES UP TO 20 YEARS: UP TO 6 YEARS FROM DIRECT OBSERVATION, THENCE BY CALCULATION

Age (years) ...	1	2	3	4	5	6	7	8	9	10
Approximate mean length (cm.)	23·8	30·6	33·0	34·1	35·5	36·2	37·1	37·8	38·5	39·1
Approximate mean weight (g.)	80	188	247	278	322	345	381	410	436	462
Age (years) ...	11	12	13	14	15	16	17	18	19	20
Approximate mean length (cm.)	39·7	40·2	40·7	41·1	41·5	41·9	42·3	42·7	43·0	43·4
Approximate mean weight (g.)	486	509	532	553	574	594	614	633	651	669

According to these calculations the single 46·1 cm. fish obtained during these investigations would be 30 years old and should weigh approximately 832 g.

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SUMMARY

Owing to the difficulty of age-determination in mackerel, the age and growth rate of these fish had not previously been satisfactorily determined.

Two schools of thought arose, one attributing a length of little over 10 cm. at the end of the first year of life, while the other ascribed lengths of up to about 25 cm. to 1-year-old fish.

The present investigation supports the second school. Direct age-readings from scales and otoliths have been made of fish up to 6 years of age, and the probable sizes at greater ages have been calculated.

There appears to be a critical change in growth characteristics at a mean length of about 29 cm., coinciding with the first ripening of the genital products.

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EXPLANATION OF PLATE I

Fig. 1. Mackerel scale showing one ring and two zones: ×55. From a fish 28 cm. in length, 9 October 1936.

Fig. 2. Mackerel scale showing two rings and three zones: ×44·3. From a fish 33 cm. in length, 8 June 1937.

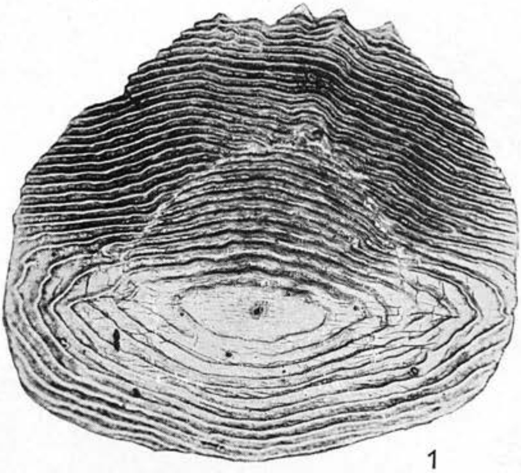
Fig. 3. Mackerel scale showing three rings and four zones: ×48·5. From a fish 34 cm. in length, 24 September 1936.

Fig. 4. Otolith showing one ring and two zones: ×12·8. From a fish 29 cm. in length, 22 September 1936.

Fig. 5. Otolith showing two rings and three zones: ×12·4. From a fish 33 cm. in length, 23 July 1936.

Fig. 6. Otolith showing three rings and four zones: ×12·05. From a fish 34 cm. in length, 22 September 1936.

The illustrations in this plate are all from un-retouched photographs.



1

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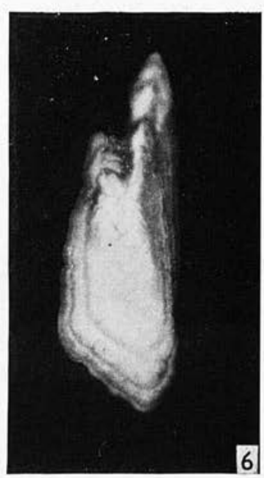

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